NUTRITIONAL AND ECOLOGICAL DETERMINANTS OF GROWTH AND REPRODUCTION IN CARIBOU

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ABSTRACT

I investigated the mechanisms by which differences in body weight and body composition (fat, protein) of female caribou (*Rangifer tarandus granti*) from the Central Arctic and Porcupine herds might determine changes in pregnancy rate and calf growth. Allometric relations between chemical components and body weight variables were highly significant, despite tremendous seasonal changes in composition. Between October 1989 and May 1990, body fat and body protein of adult females of the Central Arctic Herd declined by maxima of 45 and 29%, respectively; an additional 32% of fat was lost by July. Extensive mobilization of fat and protein indicates winter undernutrition. Marked hypertrophy of liver and kidneys in summer suggests the presence of mobilizable protein reserves. Birth weights of calves were similar between sexes, but male calves grew relatively faster during summer and were significantly heavier than females in autumn. Both fat content and growth rate of calves declined between 4 and 6 weeks post-calving, perhaps in response to insect harassment. Weight gains of wild calves were greatly reduced or absent after 100 d of age, while captive calves continued to grow until 175 d, suggesting that first-summer growth of caribou is determined in part by nutrient availability. Birth weight and growth rate of wild calves from birth to 3-4 weeks of age accounted for nearly 79% of the variability in autumn weights, again implying summer nutrient limitation. Female caribou were unable to entirely compensate for the metabolic and ecological costs of lactation: in autumn, lactating females had 42% less fat and 9% less protein than nonlactating females. Unlike females from the Central Arctic Herd, those from the Porcupine Herd did not demonstrate compensatory weight gains over summer; instead, autumn weight was highly correlated to June weight. Probability of pregnancy was positively correlated with body weight and fat content in early winter. Females that extended lactation into November were less fertile than predicted by body size or condition. I believe that these females were exhibiting lactational infertility.

TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

TABLE OF CONTENTS (continued)

LIST OF FIGURES

LIST OF TABLES

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A special thanks to Dr. Robert G. White of the Institute of Arctic Biology and Dr. Raymond D. Cameron of the Alaska Department of Fish and Game for inviting me to the University of Alaska Fairbanks and co-chairing my committee. Dr. White, with his creative suggestions, in-depth knowledge of ruminant physiology and ecology, and endless enthusiasm added zest to my research and provided alternative perspectives to data interpretation. Dr. Cameron, in turn, provided invaluable logistical support, thorough editing of proposals and papers for content and style, and a no-nonsense approach to testing of hypotheses and presentation of results. Without the assistance of these two scientists, I would not have had the opportunity, nor the experience and knowledge to conduct this research.

When I came to Alaska in 1989, I began a study on measurement of body composition of free-ranging caribou using marker dilution techniques. Although I did not include results from the water dilution trials in my dissertation, they were the starting point from which my research developed. I initially determined chemical body composition of adult female caribou from the Central Arctic Herd to validate water dilution techniques and body condition scores. The need for a more controlled study and a complete water dilution curve led to captive studies on reindeer, which I initiated and supervised to completion in spring 1990. A subsequent change in policy at the Alaska Department of Fish and Game restricted the use of tranquilizing drugs in the Central Arctic or Porcupine Herds, and we were unable to continue the application of dilution techniques in the field.

The study of calf growth in relation to maternal condition developed from a series of conversations between myself and Dr. D. Brad Griffith of the U.S. Fish and Wildlife Service, Don E. Russell of the Canadian Wildlife Service, and Drs.White and Cameron. My interest in nutrient allocation between maternal tissues and reproduction complemented Dr. Griffith's proposed study of habitat use and body growth of Porcupine

caribou calves. Dr. Griffith and I both used body weight data collected from radio-collared calves in 1992, and I collected body weight data on their mothers, in cooperation with Don Russell. Because no publication detailed the relation between chemical composition and body weight in growing caribou calves, I also initiated the study of chemical composition in juvenile caribou.

Don Russell kindly invited me to assist him with his study of autumn pregnancy rates in the Porcupine Herd. He sent Debbie Wetering and myself into the field in November 1990, to apply body condition scores and collect body weights, and blood and milk samples. When the data from the first capture effort looked promising, he joined us for 2 subsequent field seasons, from which I developed a model predicting pregnancy rates from autumn body condition and lactational status of females.

I was involved in all aspects of study design and data collection for the determination of chemical composition in caribou and reindeer, and the relations between maternal condition and calf growth in wild caribou. While the initial design of the pregnancy study was concluded before my involvement, I provided input during subsequent seasons, devised and applied the body condition score, and insisted that milk be collected from all females captured. I performed or supervised all laboratory analyses, except the determination of progesterone concentrations, which were analyzed at Colorado State University. I conducted all statistical tests, drafted all figures, and subsequently wrote each manuscript, incorporating the comments of my co-authors on each draft.

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Schimel assisted with laboratory analyses. Dr. Cameron, Bruce Gilmore, Dr. Brad Griffith, Grant M. Lortie, Dr. Tom R. McCabe, Dr. Walter Smith, and Kenneth R. Whitten captured wild caribou with dart or net guns. Dr. Cameron, Jim Henderson, Dennis C. Miller, Ron M. Warbelow, Delmar Washington, Ken Williams and Jon Wytham served as pilots during this study. Captive caribou and reindeer were housed at the Large Animal Research Station, University of Alaska Fairbanks. Caribou were ably cared for and routinely weighed by Karen Higgs, Valerie Baxter, and other LARS personnel, under the supervision of Bill M. Hauer. Assistance with reindeer was provided by personnel from Animal Quarters, under the supervision of Don Hartbauer. Without the help of these many people, I could not have accomplished nearly as much.

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Studies involving Porcupine Herd caribou were approved by the International Porcupine Caribou Herd Council. Methods of capture and euthanasia were approved by the University of Alaska Institutional Animal Care and Use Committee (IACUC # 89-013, 90-012 and 92-020).

INTRODUCTION

Rangifer tarandus is one of the most successful species of large mammals on earth in terms of current distribution and numbers (Williams and Heard 1986). Caribou and reindeer are valued for subsistence use, sport hunting, tourism, and for their role in arctic and subarctic community ecology. They exist over a wide range of latitudes and habitat-types, and are one of only two ungulate species that currently persist year-round in the high Arctic (Klein 1986), an area with wide seasonal variations in temperature, day length, weather, and food availability. The morphological, behavioral and physiological adaptations of caribou and reindeer include excellent thermal insulation (Moote 1955; Johnsen *et al.* 1985), extremely efficient locomotion (White and Yousef 1978; Fancy 1986; Luick and White 1986; Fancy and White 1987), hoof and leg morphology suited for movement and foraging through snow (Telfer and Kelsall 1984; Klein *et al.* 1987), and seasonal migrations (Kelsall 1968; Skoog 1968; Fancy *et al.* 1989). Seasonal changes in food intake (McEwan and Whitehead 1970; White *et al.* 1981), body condition (McEwan 1968; Dauphiné 1976), metabolic rate (McEwan 1970; Fancy 1986), and nutrient acquisition and utilization (White 1975, 1979, 1992; White and Luick 1976) are evidence for plasticity of the genus *Rangifer*.

Caribou numbers may fluctuate dramatically. Regular fluctuations in population size have been hypothesized from fossil evidence in Greenland (Meldgaard 1986), with dramatic changes in caribou numbers occurring every 65 to 115 y. Similarly, sudden population declines have been described for various continental herds in North America (Western Arctic, Beverley, Kamanuriak, Bluenose, Nelchina): a 50-86% decline from peak population size occurred within 3 to 15 y (see Couterier *et al.* 1990). However, knowledge of forces driving such fluctuations in caribou numbers does not allow managers to reliably predict population trends. In addition, biologists are unable to confidently assess the effects of environmental disturbances, such as global warming or

petroleum development, on population size. Nonetheless, informed management will become increasingly important as the human population of the Arctic and subarctic increases, and the impacts of hunting and industrial/urban development upon caribou populations intensify.

Population regulation

Predation and nutrition are two of the primary factors that affect population growth of large herbivores. Population growth may be limited (i.e., density-independent or density-dependent changes in population size over time) or regulated (i.e., density-dependent stabilization of population size). Ungulates may be limited by predators in some systems (Bergerud 1978; Sinclair *et al.* 1985; Skogland 1991; Seip 1992), and regulated in others (Sinclair 1989; Skogland 1991). In contrast, migratory ungulates partially escape predation, and therefore are believed to be regulated primarily by density-dependent resource limitation (Sinclair *et al.* 1985; Fryxell *et al.* 1988; Messier *et al.* 1988).

It has been hypothesized that caribou populations in North America are limited by hunters, grey wolves, and grizzly bears (Bergerud 1980, 1983). However, wolves are apparently unable to respond numerically to large migratory herds of caribou in the tundra and tundra-forest ecosystems, perhaps because of the absence of alternative prey species when caribou are not present locally (Messier *et al.* 1988). By migrating to calving areas north of tree-line, caribou largely escape predation in late spring and early summer, since wolves are unable to follow with their sedentary pups (Messier *et al.* 1988). Therefore, limitation of caribou populations may be similar to that of African wildebeest (Sinclair *et al.* 1985), in that only resident herds are susceptible to limitation by predators, while herds with long migrations are less vulnerable because they are absent during part of the year. Indeed, migratory populations of caribou that calve north of tree-line (e.g., the George

River, Porcupine, and Western Arctic caribou herds) have shown dramatic increases in numbers without predator control (Davis *et al.* 1980; Messier *et al.* 1988; Fancy *et al.* 1994) and are therefore not likely limited by predators.

Where predators are scarce or absent, population regulation is expected to occur through density-dependent factors. While density-dependent regulation appears to have an intrinsic genetic or physiological basis in numerous small mammals, those same responses in large mammals appear to be a consequence of extrinsic factors (Caughley and Krebs 1983), such as disease, predation, and, most often, resource limitation (e.g., Albon *et al.* 1983a; Skogland 1983; Clutton-Brock *et al.* 1985, 1987; Klein 1985). In addition, ungulate populations become more vulnerable to stochastic weather events as they approach the carrying capacity (Klein 1968; Reimers 1984; Skogland 1985; Fowler 1987); that is, high-density populations respond more dramatically to density-independent events. While long-term studies are necessary to document density-dependency in large mammals, short-term studies can identify density-independent nutritional responses, such as those associated with deep snow or summer drought. Since the physiological mechanisms underlying density-dependent and density-independent responses to nutrition appear to be identical in large mammals (Caughley and Krebs 1983), short-term studies can delineate the mechanisms by which ungulates might respond to changes in density. Such physiological responses can then be investigated in the context of density-dependence, upon collection of long-term data.

Density-dependent responses in populations of large mammals have been summarized by Fowler (1987). They include reduced survival of neonates, juveniles, and adults; reduced body size and growth rates; changes in timing of conception or birth; and reduced conception rates. However, density-dependent responses to nutrition in populations of caribou or reindeer exposed to large predators are rarely documented. To date, only the Central Arctic and George River herds are believed to be food-limited

(Messier et al 1988; Skogland 1991; Crête and Huot 1993; Crête *et al.* 1993; Cameron 1995) while coexisting with wolves, bears, and human hunters. Nonetheless, in the absence of predators, other factors, including intra-specific competition for food, have been shown to regulate reindeer numbers via reductions in pregnancy rate of subadults (Leader-Williams 1980; Reimers 1983; Skogland 1985), lowered calf survival (Haukioja and Salovaara 1978; Skogland 1984, 1985, 1990), increased age-at first reproduction (Skogland 1985) and increased adult mortality during severe winters (Klein 1968; Reimers 1984).

Methods of determining nutrient availability

Managers frequently suspect that reduced population growth may be due to inadequate nutrient availability. However, in spite of the considerable theory on interactions between habitat quality, density-dependent population regulation, and performance of individual animals, there is considerable disagreement as to how differences in habitat quality and carrying capacity affect population performance. In addition, demonstration of nutrient limitation of a population may require habitat assessment in various seasons over several years, which may be prohibitively expensive.

One alternative to direct measurement of habitat quality is an assessment of body reserves of individual herbivores (Klein and Straandgard 1972; Dauphiné 1976; Reimers 1984). Heavier, fatter animals would theoretically indicate superior habitats. However, body weight and condition of cervids vary not only with nutrient intake and season, but also with reproductive status. The latter source of variation complicates efforts to assess interactions between body condition, range quality, and herd productivity; nevertheless, with adequate knowledge of physiological mechanisms and individual reproductive status, nutrient availability can be evaluated.

Body condition cycles

Caribou, like many cervids, demonstrate a seasonal cycle of condition and growth. These cyclical patterns were first demonstrated in white and black-tailed deer (French *et al.* 1956; Silver and Colovos 1957; Wood *et al.* 1962) and are characterized by loss of condition over winter, even in the presence of ad libitum, high-quality food, followed by regain of body weight and condition during summer (Wood *et al.* 1962; McEwan and Wood 1966; McEwan 1968).

The body condition cycle has been interpreted as an adaptive strategy. Cervids metabolize body reserves during predictable periods of food shortage, thus lowering energy costs of foraging, and permitting a less-negative energy balance. They are therefore able to exploit seasonally harsh environments that have large changes in nutrient availability (Wood *et al.* 1962; O'Donovan 1984; Moen 1985). Cervids appear to change strategies of energy acquisition during summer to achieve a set-point of body weight or fatness in autumn (Wood *et al.* 1962; Mrosovsky and Powley 1977), then conserve energy during seasons when food is scarce or of low quality. Deer on poor feeds during winter demonstrate superior gains in summer when compared to deer maintained on high quality, free-choice feed (Renecker and Samuel 1991); conversely, the magnitude of winter weight loss appears to be affected by availability of resources during the previous summer (French *et al.* 1956; Nordan *et al.* 1968). Such patterns of gain suggest that weight changes may be compensatory (Renecker and Samuel 1991) or that there is a defended or seasonally changing functional set-point for body weight (Ryg 1983; Cameron and White 1995).

Closely associated with seasonal changes in body weight and condition are changes in metabolic rate and voluntary food intake. Seasonal changes in dry matter intake are well documented in captive cervids (French *et al.* 1956; Silver and Colovos 1957; Wood *et al.* 1962; Nordan *et al.* 1968; Bandy *et al.* 1970; Nilssen *et al.* 1984); voluntary intake increases in summer, and declines in winter. Changes in fasting metabolic rate,

approaching 80% higher in summer than in winter (Silver *et al.* 1969, 1971; McEwan and Whitehead 1970; Thompson *et al.* 1973; Holter *et al.* 1976), have been proposed as the primary controlling mechanism of the seasonal body weight and condition cycle, and have been interpreted as a unique adaptation for survival during seasonal periods of energy-limitation (Moen 1985). However, existence of seasonal changes in basal metabolic rate in cervids has recently been challenged (Mautz *et al.* 1992), as has the role of reduced resting-metabolic rate as an adaptive strategy to conserve energy in winter (Nilssen *et al.* 1984).

Fatness is an index of an animal's recent energetic balance and of its ability to cope with future energetic demands. Until recently, loss of body fat was thought to be the principle cause of overwinter weight reductions in mature cervids (Anderson *et al.* 1972; Dauphiné 1976; Mitchell *et al.* 1976). While most weight changes in mature male caribou and reindeer may be attributed to changes in body fat (Reimers *et al.* 1982), recent studies have shown that loss of fat in female deer and fawns accounts for as little as 31% of overwinter weight loss (Huot 1982), while 23-31% of weight loss may be attributed to body protein (Huot 1982; Torbit *et al.* 1985).

The role of body protein in cervids has received less attention than that of fat and is therefore not well understood. In fact, both nitrogen and energy balance can limit growth of white-tailed deer (Seale *et al.* 1978; Verme and Ozoga 1980a); and recent studies of caribou indicate that dietary energy:protein ratios may determine rate of protein deposition in lactating caribou (Chan-McLeod *et al.* 1994), while maternal protein reserves may determine fetal growth of caribou (Allaye-Chan 1991). In addition, the amounts of energy and protein available in the diet may affect both protein deposition and lipogenesis (Jagusch *et al.* 1970; Verme and Ozoga 1980b).

Genetic and phenotypic constraints on accretion and mobilization of body reserves must be better understood in order to interpret the significance of observed levels and

changes in body condition. The amplitude of the cycle of seasonal weight gain and loss appears to be an adaptive tradeoff between the conflicting needs for mobility (e.g., Klein *et al.* 1987) and maximal reproductive fitness (e.g., Tyler 1987a) and therefore should be determined primarily by genetic makeup. Phenotypic variation will be introduced by variation in nutrient availability during the lifetime of the animal (e.g., Reimers 1983; Skogland 1985). Variability in reproductive performance at a certain body condition within a population may be caused by either genetic differences (Pemberton *et al.* 1991) or differences in nutritional history (Albon *et al.* 1987; Langvatn 1994), rather than by recent nutritional events. However, few detailed studies of reproductive variability among individual caribou or reindeer within a population have been conducted (Lenvik *et al.* 1988; Kojola 1989; Kojola and Eloranta 1989; Petersson and Danell 1993).

Mainland caribou populations demonstrate a relatively small annual amplitude in body weight and reserve cycles (Dauphiné 1976; Huot 1989; Allaye-Chan and White 1991). Apparently the necessity of cratering, moving through snow, and escaping predators has selected for long legs and a mobile lifestyle (Klein *et al.* 1987), one that is incompatible with excessive fattening. Individuals from mainland herds kept in captivity and fed *ad libitum* retain the small amplitude in seasonal weight cycles (White unpubl. data), implying that differences in potential peak body reserves between populations are primarily genetic. Indeed, genetic differences between mainland and arctic island populations have been documented (Røed and Whitten 1986; Røed 1991).

Populations of *Rangifer* living on high arctic islands (e.g. Svalbard Archipelago, Coat's Island) exhibit extreme cycles of body weight and fat reserves (Reimers 1984; Adamczewski *et al.* 1987a; Tyler 1987a). Selection for mobility has apparently been relaxed by the low snowfall and lack of predators (Klein *et al.* 1987). These populations survive at what is apparently the adaptive extreme of the species in terms of seasonal nutrient availability and energy storage capacity. They are in a negative energy balance 8-

10 months of the year (Reimers 1984; Tyler 1987a), and require an abundance of high quality summer forage (White and Stalaand 1983) to accommodate an extreme weight loss overwinter (Reimers 1983, 1984; Adamczewski *et al.* 1987a; Tyler 1987a). Yet seasonal accumulation of energy reserves, even in the extremely fat Svalbard reindeer, may provide females with only 25% of the energy expended to survive winter (Tyler 1987a). Therefore, even though these populations are regulated primarily by periodic winter starvation (Reimers 1984; Gates *et al.* 1986), accumulated body reserves may be an adaptation to enhance reproductive success (Wood *et al.* 1962; Kay 1985; Tyler 1987a), as well as to compensate for subsequent undernutrition during winter.

Reproductive tradeoffs

In long-lived animals, reproductive output reflects a trade-off between maximizing production and survival of current offspring and accruing sufficient resources to survive and reproduce again (Trivers 1974; Clutton-Brock and Godfray 1991). An individual's success in meeting these competing needs determines its lifetime reproductive output. Arctic caribou must partition resources to meet the conflicting nutritional demands of lactation and replenishment of maternal body reserves during the brief nutrient pulse of summer. Failure to provide sufficient milk may slow calf growth (Loudon *et al.* 1983a,b; Loudon and Kay 1984; White and Luick 1984) and therefore threaten calf survival overwinter (Haukioja and Salovaara 1978; Clutton-Brock *et al.* 1985), while failure to replenish maternal fat and protein depots may reduce the female's own subsequent reproductive success (see below) or survival (Albon *et al.* 1983a; Clutton-Brock *et al.* 1983).

Offspring with high rates of first-year growth are more likely to become socially dominant (males) or to begin reproducing at a young age (females). Reproductive success of male offspring in polygenous species is related to competitive ability, which, in turn, is

related to large body size and early growth (Suttie 1983; Clutton-Brock and Albon 1985). In addition, age at first reproduction in females is determined in part by growth to some critical weight (Edey 1968; Foster 1988), above which probability of ovulation and conception increases considerably (Hamilton and Blaxter 1980; Albon *et al.* 1983a, 1986; Tyler 1987b). Growth of calves during their first year largely determines the age at which individuals reach reproductive size (Tyler 1987b; Langvatn 1994) and influences maximum body size (Mitchell *et al.* 1976; Reimers et al 1983; Skogland 1983; Kay 1985; Langvatn 1994). In addition, since a successful male of a polygenous species may have greater reproductive success than the average female, mothers are expected to allocate more resources to male offspring during growth (Trivers and Willard 1973).

While calf growth is a determinant of its future reproductive success, failure to allocate sufficient resources to maternal reserves may compromise the ability of a female to reproduce the following year. Conception and ovulation rates are correlated with body condition of the female at time of breeding in domestic sheep (Edey 1968; Gunn and Doney 1973), red deer (Mitchell and Brown 1974; Hamilton and Blaxter 1980; Albon *et al.* 1983a, 1986), and reindeer and caribou (Klein and White 1978; Thomas 1982; Reimers 1983; Cameron *et al.* 1993; Cameron and Ver Hoef 1994). Therefore, lactating females that do not regain adequate body weight and condition are expected to be less fertile than their heavier or fatter counterparts.

The reproductive strategy of caribou has been characterized as conservative. Females allocate fewer resources to fetal growth per unit maternal weight than other ungulates (Robbins and Robbins 1979); nonetheless, female caribou probably optimize offspring production rather than maternal size (Skogland 1983; Crête and Huot 1993). Although post-natal growth is rapid (Parker *et al.* 1990), milk production begins to decline within 3 weeks of parturition (White and Luick 1984; Parker *et al.* 1990; White 1992; Chan-McLeod *et al.* 1994), and suckling rate declines dramatically approximately

40 d post-calving (Parker *et al.* 1990; Lavigueur and Barrette 1992). Maternal allocation priorities may switch from lactation to accumulation of maternal reserves at approximately 40 d post-calving (Cameron and Luick 1972; Ryg 1986; White and Luick 1984). Even so, summer nutrition of mainland caribou herds is often inadequate to allow lactating females to regain fat and protein reserves equal to those of females that did not lactate that summer (Dauphiné 1976; Huot 1989; Tyler 1990; Allaye-Chan 1991).

Examining nutrient availability in Rangifer

Undernutrition may affect productivity of caribou and reindeer differently depending upon the period of the year in which food shortage occurs. Skogland (1985) emphasized the importance of winter nutrition, since condition of female reindeer in late winter correlates with both body size of calves at birth and date of birth. Others have reported that maternal body weight 3-4 weeks post-calving is highly correlated with early calf survival and calving date (Cameron *et al.* 1993), and that fetal size and birth weight of caribou are correlated with maternal body protein reserves in late winter (Allaye-Chan 1991). However, summer nutrition may also be an important determinant of conception rate and calf survival (Reimers 1980, 1983). Studies of caribou demonstrate that fecundity is correlated with body weight and condition in autumn (Allaye-Chan and White 1991; Cameron *et al.* 1993; Cameron and Ver Hoef 1994).

There is no *a priori* reason to discount either summer or winter nutrition as important to productivity of mainland Alaska caribou herds (White *et al.* 1981), particularly if the relative influence of energy and protein differ with season and/or year. Inadequate nutrition during one season of the year can restrict herd productivity if it cannot be compensated for at another (Couturier *et al.* 1990; Cameron and Ver Hoef 1994). While not dismissing the importance of winter nutrition, I focus here primarily on an evaluation of summer range quality through longitudinal determinations of body

composition (i.e. fat and protein reserves) and body weight of individual calves and adult female caribou in summer and autumn.

White *et al.* (1992) hypothesized that the large, between-herd differences in average autumn weight of non-lactating females relative to lactating caribou reflects regional differences in summer range productivity. Further, the differential gain between lactating and non-lactating females within a herd may be an index of nutrient allocation to lactation; hence, autumn weight of non-lactating females should correlate with calf growth rate, since calf growth is an index of nutrient quality and availability (Kay 1985; White 1992). I suggest that the absolute body weight or condition level of adult females in autumn may not be as sensitive an indicator of summer range quality as over-summer body weight gain of nonlactating females and calves. Specifically, two populations with differences in summer range quality should exhibit differences in fatness and rate of weight gain for both non-lactating females and calves during summer and autumn.

CHAPTER 1: BODY COMPOSITION AND NUTRIENT RESERVES OF ARCTIC CARIBOU[1]

Abstract: I determined seasonal changes in body weight and composition of arctic caribou (*Rangifer tarandus granti*) in relation to age and reproductive status. Chemical composition was determined for 37 caribou calves from the Central Arctic Herd (CAH) ranging from 1 to 134 days of age, and for 15 adult females collected from the same herd in October, May, and July. Composition of 5 CAH fetuses, 13 Porcupine Herd calves, and 10 captive male reindeer (*R. t. tarandus*) was determined for comparison. Between October 1989 and May 1990, body fat and protein of adult females declined by maxima of 45 and 29%, respectively; an additional 32% of fat was lost between May and July. Mobilization of large amounts of fat and protein suggests winter undernutrition. Chemical composition and growth pattern of calves did not differ between herds. Growth rate of CAH calves was high during the first 28 d post-partum (402 g/d); but both growth rate and fatness declined between 4 and 6 weeks of age (to 306 and -18.3 g/d, respectively), perhaps in response to insect harassment. Birth weights of males and females did not differ, but, by autumn, male calves were 9.1 kg heavier than females. Chemical components (water, fat, protein, ash) were highly correlated with body weight, ingesta-free body weight and carcass weight. Percentages of fat and water were inversely related, but the intercept decreased with age. Marked seasonal hypertrophy of liver and kidneys was noted in caribou, suggesting the presence of mobilizable protein reserves. Seasonal changes in organ weights also may reflect variations in metabolic activity and nutrient intake.

[1]Gerhart, K.L., White, R.G., Cameron, R.D., and Russell, D.E. Submitted. Body composition and nutrient reserves of arctic caribou. Can. J. Zool. **00**: 00-00.

Introduction

Knowledge of growth processes of caribou and the consequences to fecundity and neonatal survival are crucial if biologists are to better understand density-dependent effects on herd productivity. Some cervids are known to regulate body weight in relation to autumn or spring set points (Ryg 1983; Hudson *et al.* 1985; Renecker and Samuel 1991; Cameron and White 1995). For adult female caribou, consistently attaining "targets" of body weight or composition will maximize lifetime reproductive success, as fertility is correlated with autumn body condition (Dauphiné 1976; Thomas 1982; Reimers 1983; Tyler 1987a; Cameron *et al.* 1993; Cameron and Ver Hoef 1994). Moreover, since growth prior to puberty is influenced directly by nutrition, growth rates of calves can be useful as indicators of nutrient availability. Calf growth during the first summer is a determinant of adult size (Loudon and Milne 1985; Skogland 1985), overwinter survival (Clutton-Brock *et al.* 1985; Haukioja and Salovaara 1978), age of first reproduction (Leader Williams and Rosser 1983), and potential reproductive success (Clutton-Brock *et al.* 1982). It should be recognized, however, that the energetic cost of growth varies with the type and composition of the tissue being deposited or mobilized (Price and White 1985).

Body fat accounts for most overwinter weight loss of female cervids (Dauphiné 1976; Mitchell *et al.* 1976), although nearly one-third of the body protein also can be catabolized (Huot 1982; Reimers *et al.* 1982; Reimers and Ringberg 1983; Torbit *et al.* 1985; Adamczewski *et al.* 1987a; Huot 1989). Excessive maternal weight loss during late gestation appears to be linked to higher rates of perinatal mortality (Rognmo *et al.* 1983; Skogland 1985; Adamczewski *et al.* 1987a; Allaye-Chan 1991; Cameron *et al.* 1993). While fat and protein reserves of female caribou are lowest approximately 3 weeks after calving (Dauphiné 1976; Adamczewski *et al.* 1987a; Allaye-Chan 1991), and highest in autumn (Dauphiné 1976; Reimers *et al.* 1983; Adamczewski *et al.* 1987a; Tyler 1987a;

Allaye-Chan 1991), changes between autumn and mid- to late winter are inconsistent. Appreciable losses of body fat prior to late winter are common for *Rangifer* populations (Dauphiné 1976; Reimers *et al.* 1982; Reimers and Ringberg 1983; Tyler 1987a; Adamczewski *et al.* 1987a), but there are exceptions (Huot 1989; Allaye-Chan 1991). Declines in body protein content have been noted for several island populations of *Rangifer* (Reimers *et al.* 1982; Reimers and Ringberg 1983; Tyler 1987a; Adamczewski *et al.* 1987a), but for only one mainland herd (Huot 1989).

The role of maternal protein in determining fetal growth and neonatal survival in *Rangifer* remains unclear. It is clear, however, that fetal body protein must be synthesized almost entirely from maternal tissues, since the amount of protein derived from a predominantly lichen diet is very low (Jacobsen and Skjenneberg 1976). Calf birth weight is correlated with maternal protein content at parturition (Allaye-Chan 1991), suggesting that maternal protein status during the previous summer is related to offspring viability. However, the site of this maternal protein reserve has not been determined.

I investigated body weight and chemical composition of calf and adult caribou to determine the extent to which allometry is maintained during seasonal weight gain and loss. Seasonal hypertrophy of intestinal organs is discussed in the context of a dual adaptation: to support summer growth, fattening, and lactation; and to provide a mobilizable protein reserve for fetal growth.

Methods

Free-ranging caribou (*Rangifer tarandus granti*) from the Central Arctic Herd (CAH) and Porcupine Herd (PCH) were used in this study. Fifteen adult female CAH caribou were shot from a helicopter in early October 1989 (n=5) and in early May and July 1990 (n = 6 and 4, respectively). Twenty-six CAH calves were collected similarly during the summer of 1992. In addition, 10 newborn CAH calves were captured by personnel on

foot and killed with a captive bolt gun, and 5 PCH calves were shot from a boat during autumn in 1992. Also included were 5 newborn caribou (4 PCH, 1 CAH) found dead shortly after birth, 5 fetuses collected from pregnant CAH females in May, and 4 PCH calves that had been injured or orphaned. Finally, 9 captive adult male reindeer (*R. t. tarandus*) and 1 captive adult male caribou/reindeer hybrid were killed in late winter, early spring, and early autumn.

Immediately after death, metatarsus length (mm) and mandible length (mm) were measured (Langvatn 1977). Fetuses, newborn and calves 3-4 week old were weighed to the nearest 50 g, while all others were weighed to the nearest 100 g. Animals either were eviscerated and processed immediately or were wrapped in 2 layers of plastic, with sealed cold packs in each abdominal cavity, and flown to Fairbanks in waxed cardboard boxes. On arrival, caribou were reweighed and skinned; hooves and heads were removed. Carcasses of adults and autumn calves were split medially down the spine. The left halves or whole carcasses were wrapped in 2 layers of plastic and frozen at -20 °C. Internal organs and alimentary tracts were weighed, emptied, rinsed, and re-weighed. All viscera were then wrapped in plastic and frozen, as above.

Frozen half-carcasses, viscera, and heads of adults were reweighed, then sliced with a bandsaw at ca. 2-cm intervals; the "dust" was collected for chemical analysis (Huot and Picard 1988). Carcasses, heads, and viscera of each calf were minced 3 times in a Toledo® meat grinder, and homogenates were sub-sampled for chemical analysis. For calves, five 100 cm^2 sections of hide were shaved and cut from each pelt. Hair and hide were weighed, freeze-dried, and analyzed for chemical composition. For adults, hair and hide composition was estimated from relations provided by J. Huot (pers. comm.).

Water content of carcasses, viscera, hides, and heads was determined in triplicate by freeze-drying samples to constant weight. Fat content was determined by petroleum ether extraction in a Soxhlet apparatus, and ash content was determined by incineration in

a muffle furnace at 500° C. Protein content was estimated by difference, verified with micro-kjeldahl analysis (agreement within 2.5%, n=25).

Ages of newborn calves were designated as 1 d, while ages of older calves were estimated by assuming birth on 5 June, the approximate peak of calving for the CAH in 1992 (R.D. Cameron, unpubl. data). Here, I define body weight (BW) as total weight less antlers, concepta, and incidental blood loss; ingesta-free body weight (IFBW) as BW less alimentary contents; and carcass weight (CW) as IFBW less head, hide, hooves and viscera. Amounts of body fat, water, ash, and protein are expressed as percentages of IFBW.

Allometric relations ($Y=aX^{b)}$ between chemical components (Y) and BW, IFBW, or CW (X) were examined after logarithmic transformation, which yielded equations in the form $Log_e(Y)=a+b*Log_e(X)$. Weighted-least squares regression (NLIN, SAS) was applied to the transformed data to stabilize variance. Differences between sexes and seasons were tested using analysis of variance for unbalanced data (GLM, SAS). Differences between intercepts and slopes were examined using analysis of covariance (GLM, SAS). Relations between weights of organs and IFBW were examined using Execustat (2.1 Student edition).

Results

Seasonal and age-related changes in body weight and composition

Mean BW of CAH caribou increased 17.5 fold, from 5.6 kg for newborns to nearly 100 kg for nonlactating adult females in autumn (Table 1). During the last month of pregnancy, mean fetal BW increased 84% and mean metatarsus length increased 30%, but mandible length increased only 16%. Birth weights did not differ between sexes, nor did growth rates differ during the first 6 weeks postpartum. Calves tripled in weight during the first 4 weeks after birth, and gained an additional 35% during the following 2.5 weeks.

Table 1. Weights and skeletal dimensions of arctic caribou and captive reindeer. Mean (± 1 SE) body weight (less antlers and concepta), ingesta-free body weight (IFBW), and skeletal measurements of caribou from the Central Arctic and Porcupine Herds, and of captive reindeer.

Subspecies, age and year	n	Body weight, kg	IFBW, kg	Mandible length, cm	Metatarsus length, cm
Caribou					
Fetuses (May 1990)	5	3.07 ± 0.12	3.07 ± 0.12	10.7 ± 0.2	18.9 ± 0.5
Dead Newborns, '92	5	4.72 ± 0.61*	4.69 ± 0.60	11.3 ± 2.9*	24.6 ± 2.9
Live Newborns, 1992	10	5.65 ± 0.21	5.47 ± 0.21	12.4 ± 0.1	24.6 ± 0.3
24-28 d calves, 1992	10	16.41 ± 0.74	15.41 ± 0.66	15.3 ± 0.2	29.0 ± 0.4
44 d calves, 1992	10	22.1 ± 1.2	19.6 ± 1.1	16.3 ± 0.3	29.4 ± 0.4
102 d calves, 1992	5	43.8 ± 2.1	37.6 ± 1.4	20.4 ± 0.3	33.7 ± 0.3
134 d calves, 1992	10	45.0 ± 2.4	37.5 ± 2.3	20.7 ± 0.4	33.7 ± 0.4
Adult ♀, Oct 1989	5	89.9 ± 3.3	74.7 ± 2.9	27.3 ± 0.2	38.5 ± 0.3*
Adult ♀, May 1990	6	68.5 ± 3.0	60.7 ± 2.6	not measured	38.7 ± 0.2
Adult ♀, July 1990	4	75.9 ± 2.1	60.9 ± 2.8	27.1 ± 0.6*	38.4 ± 0.4
Reindeer:					
♂, + 1 hybrid, 1990	10	117.6 ± 12.4	101.0 ± 12.4	not measured	34.1 ± 1.2

Note: * Sample size is n-1

By autumn, calves were 800% heavier than when born, and males were 9.1 kg heavier than females ($P = 0.004$). BW and skeletal dimensions for the CAH calves at 134 d of age were similar to, but more variable than for PCH calves at 102 d.

As animals matured, the percentage of weight gained as ash, protein, and fat increased, while that gained as water decreased (Fig. 1). Ash content increased until IFBW reached 70 kg and then stabilized. The relation between protein content and IFBW was similar, but at high levels of body fat (>10%), the relationship became curvilinear, as noted for sheep (Reid *et al.* 1968). Percentages of fat and water were inversely related (Fig. 2), and the slope of the regression was the same for all animals > 1 week of age (-1.125, $P = 0.11$). However, the X-intercept increased significantly with age class ($P = 0.0001$): at 0% fat, estimated percentages of water were 68.6 for adults, 71.7 for calves 15-19 weeks old, and 74.8 for calves 3-6 weeks old. No relation between the percentages of fat and water could be detected among calves < 1 week of age ($P > 0.05$; mean water and fat content were 75.8 ± 0.3% and 2.0 ± 0.2%, respectively). Mean percentage water declined 8.7% during first-summer growth, while percentage protein and ash increased 4.0 and 1.2%, respectively, and body fatness (1.9 to 6.1%) varied through approximately the annual range observed for lactating adult female caribou (Table 2). Calves were especially lean at 6 weeks of age (1.9 ± 0.2% fat), and were fattest in autumn (6.1 ± 0.6%). Among calves ≤ 6 weeks of age, fat content of female calves was 1.2% higher than that of males ($P = 0.03$), while in autumn ash content of males was 0.6% higher than that of females ($P = 0.005$). BW and body composition of calves at 102 and 134 d did not differ independently of sex ($P = 0.68$). First-summer growth (% change in BW) was attributable to increases of water (52.1%), protein (20.5%), fat (5.3%), ash (4.7%), and alimentary fill (17.4%).

For adult females, peaks of BW, IFBW, and fat and protein content occurred in autumn (Tables 1 and 2). Nonlactating females were nearly 42% fatter but only 9% higher

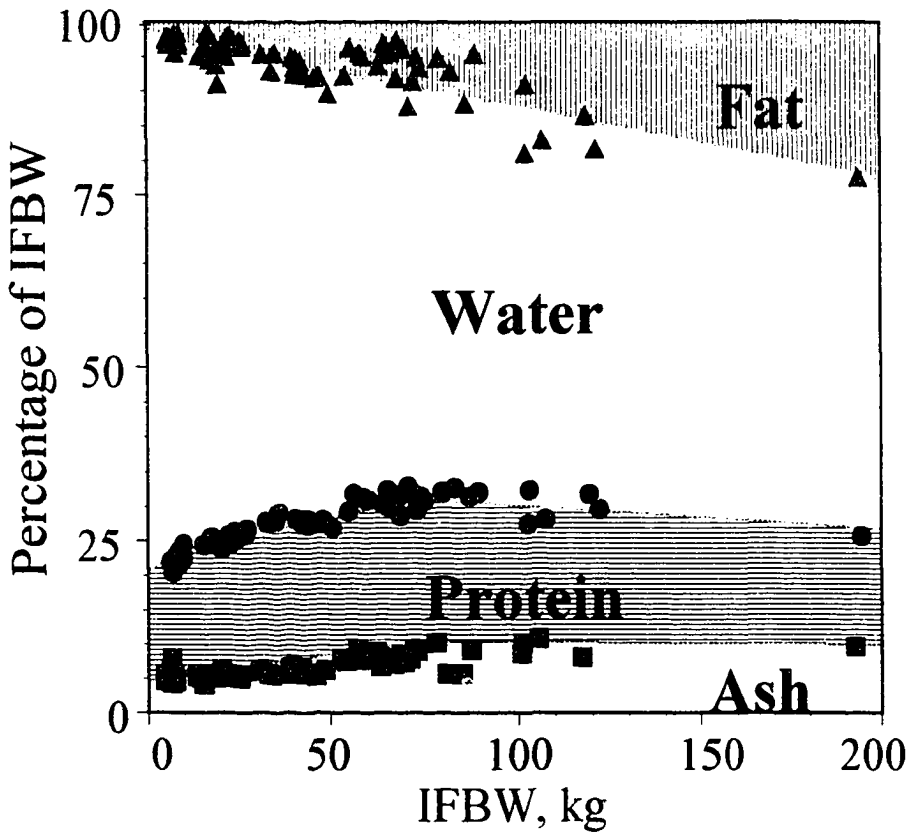

Figure 1. Proportional chemical composition of the ingesta-free body. Percentages of ingesta-free body weight (IFBW) comprised of fat, water, protein and ash in growing arctic caribou and mature arctic caribou and reindeer.

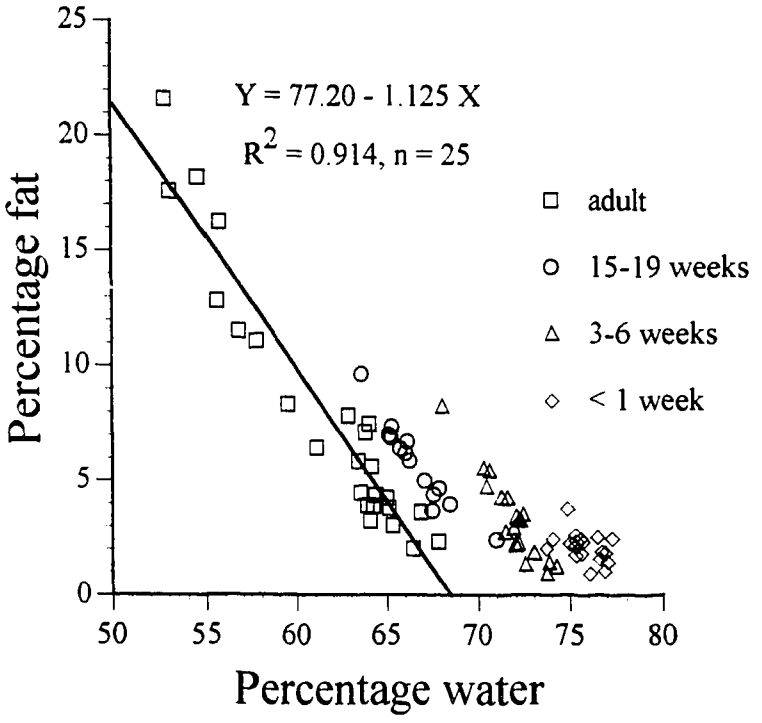

Figure 2. Relation between the percentages of fat and water in the ingesta-free body of caribou and reindeer at various ages. Regression equation shown is for adults weighing 56 - 191 kg. Y-intercepts for calves are 80.64 (15-19 weeks of age), 84.12 (3-6 weeks), and 87.29 (< 1 week).

Table 2. Chemical composition of caribou and reindeer. Mean (± 1 SE) chemical composition of the ingesta-free body (IFB) for calf and adult female caribou of the Central Arctic Herd (CAH) and Porcupine Herd (PCH), and for captive male reindeer.

Age or reproductive class	n	IFB water, kg (%)	IFB fat, kg (%)	IFB protein, kg (%)	IFB ash, kg (%)
Fetuses CAH	5	2.36 ± 0.09 (76.83 ± 0.14)	0.06 ± 0.01 (2.01 ± 0.19)	0.51 ± 0.02 (16.78 ± 0.29)	0.13 ± 0.01 (4.38 ± 0.23)
Dead Newborns CAH & PCH	4	3.6 ± 0.5 (76.4 ± 0.4)	0.11 ± 0.01 (1.2 ± 0.2)	0.95 ± 0.04 (17.9 ± 0.1)	0.21 ± 0.04 (4.5 ± 0.3)
Live Newborns CAH & PCH	10	4.1 ± 0.2 (75.1 ± 0.2)	0.13 ± 0.01 (2.4 ± 0.2)	0.99 ±0.04 (18.0 ± 0.1)	0.25 ± 0.02 (4.5 ± 0.2)
24-28 d (3-4 wk) CAH & PCH	10	10.9 ± 0.5 (71.2 ± 0.4)	0.71 ± 0.09 (4.6 ± 0.5)	3.0 ± 0.1 (19.4 ± 0.1)	0.76 ± 0.04 (4.95 ± 0.07)
44 d (6 wk) CAH	10	14.2 ± 0.7 (72.7 ± 0.3)	0.38 ± 0.05 (1.9 ± 0.2)	4.0 ± 0.2 (20.4 ± 0.1)	1.00 ± 0.07 (5.07 ± 0.09)
102 d (15 wk) PCH*	5	25.1 ± 0.8 (66.9 ± 0.5)	2.0 ± 0.3 (5.1 ± 0.6)	8.4 ± 0.2 (22.4 ± 0.3)	2.1 ± 0.1 (5.6 ± 0.2)

Table 2 (continued)

134 d (19 wk)	10	24.8 ± 1.4	2.4 ± 0.4	8.2 ± 0.5	2.1 ± 0.2
CAH*		(66.4 ± 0.7)	(6.1 ± 0.6)	(21.9 ± 0.2)	(5.6 ± 0.2)
Lactating ♀	3	43.3 ± 2.2	5.01 ± 1.5	17.9 ± 0.4	4.1 ± 0.4
CAH, October		(61.6 ± 2.4)	(7.2 ± 2.2)	(25.4 ± 0.8)	(5.8 ± 0.6)
Nonlactating ♀	2	48.4 ± 0.2	7.1 ± 2	19.5 ± 0.3	6.5 ± 0.3
CAH, October		(59.5 ± 1.7)	(8.7 ± 2.3)	(23.9 ± 0.1)	(8.0 ± 0.5)
Pregnant ♀	5	39.3 ± 1.9	3.9 ± 0.5	13.8 ± 0.7	4.6 ± 0.7
CAH, May		(63.8 ± 0.2)	(6.3 ± 0.7)	(22.5 ± 0.5)	(7.4 ± 0.3)
Nonpregnant ♀	1	36.6	2.4	13.2	4.1
(Lactating)		(65.0)	(4.20	(23.5)	(7.3)
CAH, May					
Lactating ♀,	4	40.6 ± 2.1	1.6 ± 0.2	14.4 ± 0.7	4.2 ± 0.1
CAH, July		(66.7 ± 0.5)	(2.7 ± 0.4)	(23.7 ± 0.4)	(6.9 ± 0.2)
Reindeer, adult	10	58.3 ± 5.5	13.1 ± 3.9	21.0 ± 1.8	9.0 ± 1.0
♂ + 1 ♂ hybrid		(58.9 ± 1.6)	(11.0 ± 2.2)	(21.3 ± 0.7)	(8.9 ± 0.3)

Note: * Combined for calculations involving calves in autumn (means in each column not significantly different)

in protein than lactating females. In late winter (early May), pregnant caribou were 45% lower in body fat and 29% lower in body protein than nonlactating females in autumn. Mean IFBW in May was comparable to that in July, although fat content was at minimum levels in July; protein content had increased only slightly. Skeletal dimensions did not vary between seasons ($P > 0.1$).

Captive male reindeer were fatter than CAH caribou in all seasons (Table 2). Young (1.5-y) reindeer were 0.9 kg fatter in spring than lactating caribou were in July, and mature male reindeer were consistently fatter than the fattest female caribou. In autumn, the caribou/reindeer hybrid was 8 times fatter than lactating caribou.

Relations between chemical composition and weight variables

BW, IFBW, and CW were allometrically related (footnote, Table 3), and variances of the relations increased with age. IFBW ranged from 77.0 to 98.5% of BW, averaging 84.8% for adults and 91.8% for calves; CW ranged from 65.3% for 3 weeks old calves to 50.4% for adult females in July, averaging 57.5% of BW. Ingesta weight increased from 3.2 ± 1.0% of BW for newborns to 17.0 ± 3.4% for calves in autumn. Among adult female caribou, ingesta accounted for 18.3 ± 2.7% of BW, although small seasonal differences in alimentary fill were observed. Alimentary fill of reindeer that were fed concentrate averaged 15.0 ± 2.7%.

Body water, protein, fat and ash were highly and allometrically related to BW (Fig. 3), IFBW and CW (Table 3); correlations for body fat were poorest. Relations did not differ between CAH and PCH calves nor between adult caribou and reindeer, except as noted below. Adding a binary variable distinguishing non-ruminating neonates from older calves and adults in equations provided more accurate predictions of chemical composition in some cases (r = 0.939-0.999, Table 3). Body protein content (kg) of reindeer was nearly 35% higher than the peak protein content of female caribou, reflecting

Table 3. Prediction of chemical composition from weight variables. Relationships between chemical components of the ingesta-free body (Y, kg) of caribou and reindeer, and body weight (BW), ingesta-free body weight (IFBW) or carcass weight (CW, kg); presence or absence of rumen function (X_2), and sex (X_3) were offered as binary covariates.

Item	n	Component (Y)	Predictive Equation	Correlation coefficient	SQRT (MSE)
BW as X_1 (kg)			**Weighted Least-squares regression [1/Log$_e$(BW)]**		
Calf and adult caribou and reindeer	79	Water	$Log_e(Y) = -0.3801 + 0.8639\ Log_e(X_1) - 0.5437\ X_2$	0.999	0.023
		Protein	$Log_e(Y) = -1.8051 + 1.0333\ Log_e(X_1)$	0.999	0.034
		Ash	$Log_e(Y) = -3.6244 + 1.1929\ Log_e(X_1) + 0.2473\ X_2 - 0.0804X_3$	0.999	0.077
		Fat	$Log_e(Y) = -4.5223 + 1.3444\ Log_e(X_1)$	0.939	0.298
IFBW as X_1 (kg)			**Weighted Least-squares regression [1/Log$_e$(IFBW)]**		
Calf and adult caribou and reindeer	79	Water	$Log_e(Y) = -0.0589 + 0.9032\ Log_e(X_1) - 0.0764\ X_2$	0.999	0.019
		Protein	$Log_e(Y) = -1.8667 + 1.0900\ Log_e(X_1)$	0.999	0.037
		Ash	$Log_e(Y) = -3.6751 + 1.2513\ Log_e(X_1) + 0.2084\ X_2 - 0.0673\ X_3$	0.999	0.070
		Fat	$Log_e(Y) = -4.6168 + 1.4227\ Log_e(X_1)$	0.971	0.290

Table 3 (continued)

CW as X_1 (kg)			Weighted Least-squares regression [1/Log_e(CW)]		
Calf and adult	79	Water	$Log_e(Y) = 0.3296 + 0.9013\ Log_e(X_1)$	0.999	0.041
caribou, and		Protein	$Log_e(Y) = -1.4126 + 1.0920\ Log_e(X_1) + 0.1065\ X_2$	0.992	0.064
adult reindeer		Ash	$Log_e(Y) = -3.1979 + 1.2549\ Log_e(X_1) + 0.3679\ X_2$	0.995	0.105
		Fat	$Log_e(Y) = -4.4148 + 1.5386\ Log_e(X_1) + 0.4943\ X_2$	0.976	0.330

Note: X_2 = 1 for fetuses and newborns, 0 for all others; X_3 = 0 for males, 1 for females.

$Log_e(IFBW) = 0.0581 + 0.9475\ Log_e(BW)$, r = 0.999, $\sqrt{MSE}$ = 0.023, n = 78

$Log_e(CW) = -0.2673 + 0.9215\ Log_e(BW) - 0.1461\ X_2$, r = 0.999, $\sqrt{MSE}$ = 0.044, n = 79

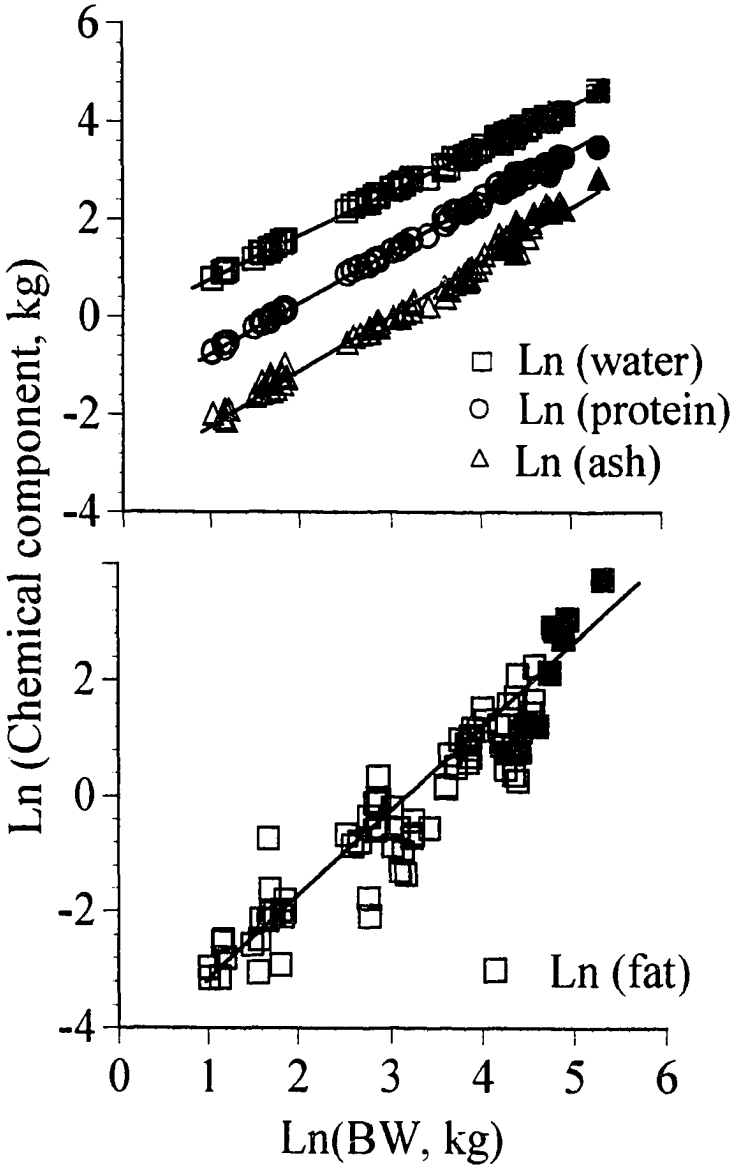

Figure 3. Relations between chemical components and body weight (BW) for arctic caribou (open symbols) and reindeer (closed symbols). Equations are given in Table 3.

the larger body size of adult male reindeer and the allometric relation between body protein and IFBW. Relations for male reindeer were not significantly different from those of female caribou, except that the former animals were significantly higher in ash per unit BW (or IFBW) than the latter; in autumn, male caribou calves also were higher in ash content than female calves. No differences between sexes or subspecies were discernible for relations between body composition and CW, perhaps because of the exclusion of heads, given that skulls were thicker for males than for females ≥ 15 weeks of age (K.L. Gerhart, pers. obs.).

Hide weight was correlated with IFBW ($r = 0.97$). Among calves, dry weight of hair accounted for 50-68% of hide weight and approximately 8.2% of body protein (range 3 - 14%). Hair comprised 7.31 ± 1.87% fat, 1.99 ± 0.36% ash, and 90.70 ± 1.88% protein.

Seasonal and age-related changes in organ weights

For adult female caribou, weights of selected organs and gastro-intestinal tissues changed dramatically with season (Table 4). Liver, kidneys, heart, gastro-intestinal (GI) tract, and total viscera weighed least in May and most in either July or October. Liver and kidneys attained maximum weight in July, while heart and GI tract were heaviest in October. Total visceral protein content (kg) was highest in July or October, and lowest in May.

When weights of kidneys and liver were plotted against IFBW, sigmoidal increases were noted for calf caribou (Fig. 4a,b). Values for adult female caribou in May were extensions of the respective relations for calves. The combined data yielded asymptotes of 0.15 and 1.0 kg for kidneys and liver, respectively. Marked seasonal maxima at approximately twice the asymptotic weight were observed in July, while weights were intermediate in October. For reindeer, organ weights were linearly related to IFBW.

Table 4. Seasonal changes in weight and protein content of organs from caribou. Changes in mean (± 1 SE) weights of selected organs, the empty gastro-intestinal (GI) tract, total viscera, and visceral protein content for adult female caribou of the Central Arctic Herd.

Season	n	Liver, kg	Kidneys, kg	Heart, kg	GI tract, kg	Total viscera, kg	Visceral protein, kg
October	5	1.54 ± 0.07^{a}	0.23 ± 0.02^{a}	1.33 ± 0.11^{a}	7.0 ± 0.2^{a}	12.6 ± 0.7^{a}	**2.9 ± 0.2^{a}**
May	6	0.84 ± 0.04^{b}	0.15 ± 0.01^{b}	0.82 ± 0.04^{b}	3.9 ± 0.2^{b}	7.1 ± 0.3^{b}	**$1.9 \pm 0.1^{b*}$**
July	4	1.84 ± 0.06^{a}	0.33 ± 0.01^{c}	0.93 ± 0.07^{b}	6.8 ± 0.5^{a}	11.6 ± 0.5^{a}	**2.9 ± 0.2^{a}**
% increase		200	220	160	180	180	**150**

^{a,b,c} Means with different letters within a column are significantly different ($P<0.05$).

*sample size equals n-1.

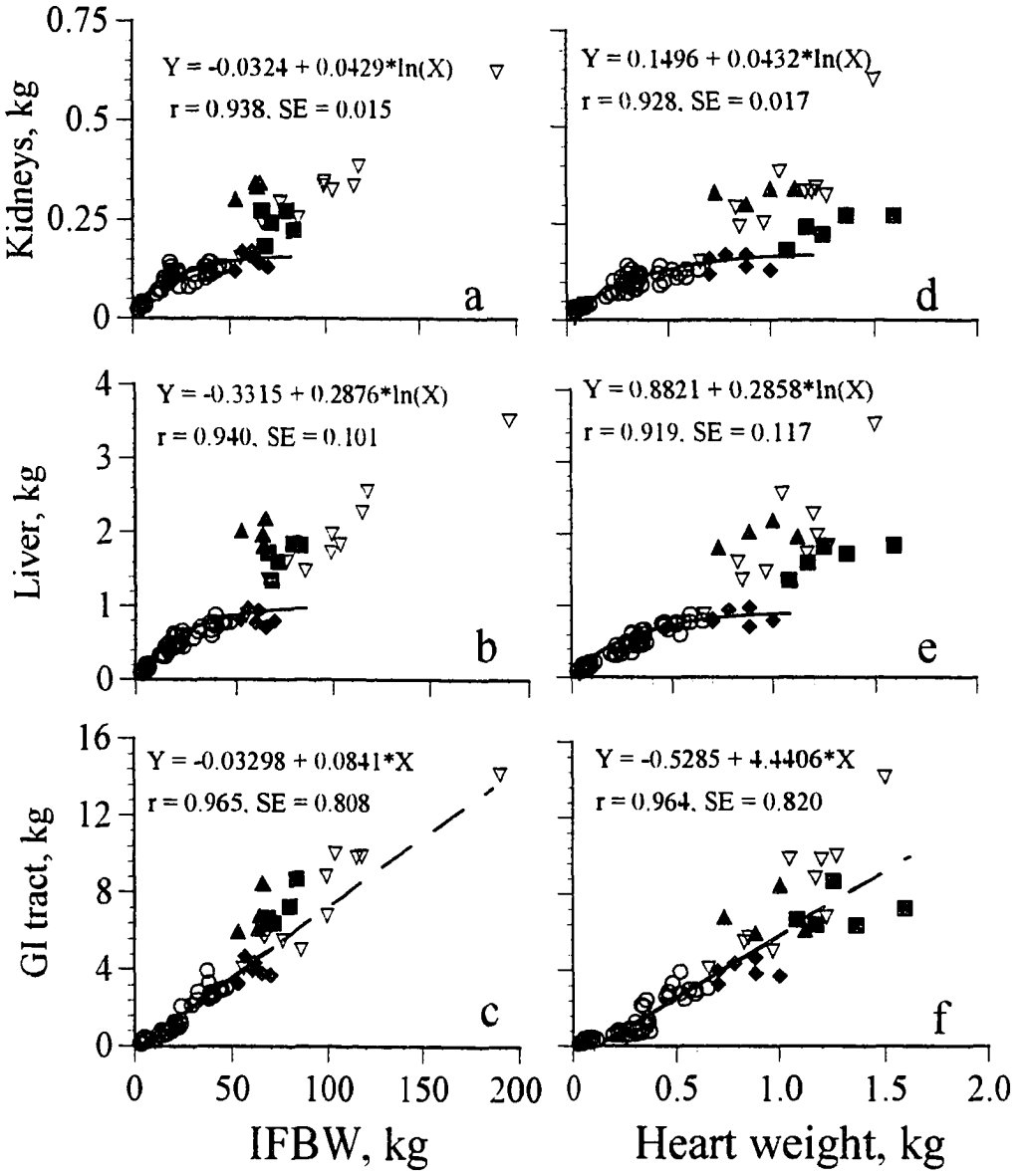

Figure 4. Seasonal hypertrophy of organs in caribou. Weights of kidneys, liver, and empty gastro-intestinal (GI) tract in relation to both ingesta-free body (IFBW) and heart weight for caribou calves (circles), adult female caribou in May (diamonds), July (triangles), and October (squares), and for male semi-domestic reindeer (inverted triangles). Curves approximate equations given above.

Weight of the empty GI tract was linearly related to IFBW for both caribou and reindeer (Fig. 4c).

Weights of kidneys and liver were directly related to heart weight as well (Fig. 4d,e). For caribou, a sigmoidal increase was apparent, except in July and October (as above), indicating >50% hypertrophy. Kidneys and livers of reindeer were also hypertrophied. As for relations based on IFBW, weight of the GI tract was linearly related to heart weight (Fig. 4f). Additionally, a tight stoichiometric relation was noted between the weights of kidneys and liver ($r = 0.99$, $P<0.001$).

The relation between heart weight and IFBW varied with age and subspecies (Fig. 5). For calves < 50 kg IFBW, heart weight was directly related to IFBW ($r = 0.96$). Separate relations were observed for adults, however. The increase in heart weight of adult caribou (21 g/kg IFBW) was 3 times that for reindeer (6 g/kg IFBW). For caribou calves, the increase was intermediate (13 g/kg).

Mean heart weight of calves was highest at 1.4% of BW. Adult heart weight averaged 1.3% of BW for caribou and 0.94% of BW for reindeer.

Discussion

The chemical composition of caribou reported here should be reasonably representative of the CAH and PCH at large. BWs of adult female caribou (Table 1) collected in October and July are similar to those from larger samples of CAH females captured in those same months as part of another study (88.8 ± 1.6 kg and 79.3 ± 1.1 kg, respectively; Cameron *et al.* 1993); and BWs of females collected in May are similar to those of another 5 females captured concurrently (73.6 ± 2.9 kg, K.L. Gerhart, unpubl. data). Also, BWs of CAH and PCH calves at various ages are representative of a larger sample of PCH calves captured 1-3 d after birth and recaptured during the subsequent summer and autumn (Chapter 4).

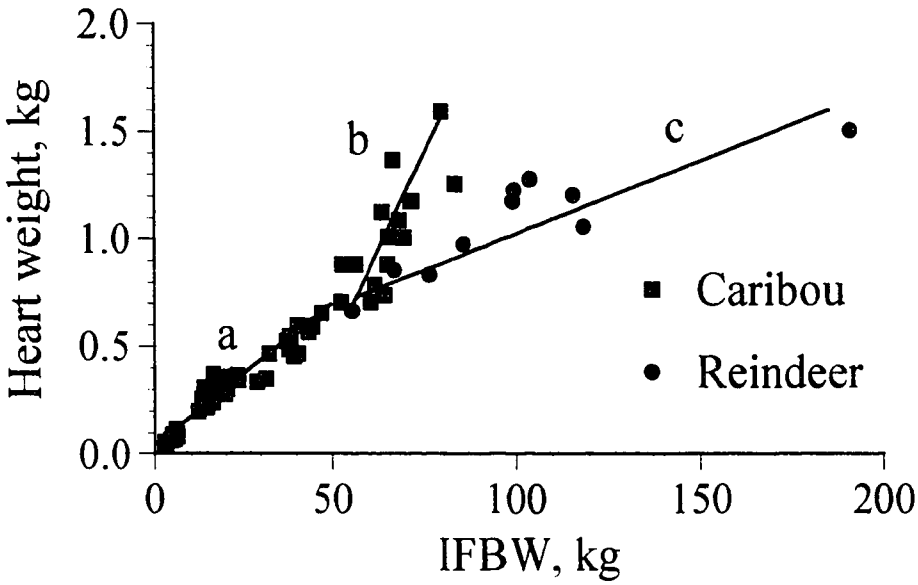

Figure 5. Relations between heart weight and ingesta-free body weight (IFBW) for calf caribou (a) and adult caribou (b) and reindeer (c):

a. $Y = 0.0310 + 0.0127\ X$, $r = 0.97$, $n = 46$;

b. $Y = -0.5731 + 0.0213\ X$, $r = 0.73$, $n = 15$;

c. $Y = 0.4817 + 0.0058\ X$, $r = 0.88$, $n = 10$.

Changes of body weight and composition during winter

Data on changes in body composition suggest that CAH caribou were protein-deficient during the winter of 1989-90. Protein content of pregnant CAH females in May was 5.7 kg lower than that of nonlactating females during the previous autumn, a maximum reduction of ca. 29%. Mammals probably cannot survive more than a 33% loss of body protein (Cahill 1970). In *Rangifer*, the winter diet is low in protein, and endogenous nitrogen excretion via urine and feces is a major factor in protein economy. For example, reindeer on predominantly lichen diets excrete nitrogen at 2.6 g/d (equivalent to ca. 16 g protein/d) (Syrjälä-Qvist and Salonen 1983), as do those on diets of low digestibility (Cameron 1972). Assuming that caribou lose protein at a rate similar to reindeer and that protein balance is negative for 7 months, nitrogen excretion accounts for 3408 g protein (16 g protein/d * 213 d), or ca. 60% of the observed loss of maternal protein overwinter. Allocation of protein to the fetus and associated tissues is an additional 13% (Table 2; protein content of uterus and associated fluids estimated from Huot 1989). Hence, our results suggest that protein loss among some CAH females in 1989-90 approached the upper physiological limit.

Protein probably was not severely limiting for the CAH in 1991-92. Otherwise, one would expect lower birth weights of calves through an effect on maternal protein reserves during late gestation (Allaye-Chan 1991; Allaye-Chan and White 1991). Weights of newborn CAH and PCH calves were, in fact, similar (Chapter 4), and, although lower than those reported for the PCH a decade earlier (Whitten *et al.* 1992), were within the general range reported for arctic caribou (McEwan 1968).

Neither was there any evidence for retardation of fetal growth which, for undernourished reindeer, occurs during the last trimester of pregnancy (Rognmo *et al.* 1983; Skogland 1984). Assuming that fetal weight in May 1992 was similar to that in May 1990, I calculated linear growth rates from early May to birth for 1992 as 81 g/d.

Even though fetal growth normally accelerates from 40 to 160 g/d during the last 30 d of gestation (Roine *et al.* 1982), this linear estimate compares favorable to the 83 g/d computed for reindeer over the same period (estimated from Roine *et al.* 1982). Moreover, composition of fetuses from the CAH was similar to that reported previously for other cervids at similar stages of gestation (Robbins and Moen 1975; Reimers *et al.* 1982; Huot 1989).

Patterns of fat use among CAH females during the winter of 1989-90 also suggest extreme food limitation. Fatness of CAH females entering that winter was similar to previous estimates for females of the PCH (Allaye-Chan 1991) and George River Herd (Huot 1989). However, CAH females had mobilized 45% of their fat reserves by late winter, while females of the PCH and George River Herd had lost no fat between autumn and early spring. The extent of fat mobilization for CAH females more closely resembles that of island populations of *Rangifer*, which draw heavily on fat reserves throughout winter (Reimers *et al.* 1982; Adamczewski *et al.* 1987a). Differences in winter nutrition are implied. The CAH has greatly expanded its winter range in recent years (Cameron, unpubl. data), possibly in response to inadequate forage (Duquette and Klein 1987; Messier *et al.* 1988), whereas the winter ranges of the PCH and George River Herds have not increased in size and reportedly have adequate lichens (Couterier *et al.* 1990; Russell *et al.* 1993).

Changes of body weight and composition during summer

Female caribou of the CAH were unable to compensate entirely for the costs of gestation and lactation. In autumn, lactating females had 2.1 kg less fat and 1.6 kg less protein than nonlactating females (Table 2), in general agreement with results from other herds (Dauphiné 1976; Huot 1989; Tyler 1990; Allaye-Chan 1991). Insufficient recovery of body reserves during summer and early autumn decreases the probability that a female

will become pregnant (Dauphiné 1976; Reimers 1983; Cameron *et al.* 1993) or survive overwinter (Clutton-Brock *et al.* 1985; Price and White 1985).

Growth patterns for CAH calves suggest a mid-summer period of nutrient shortage. Fat content of calves decreased from 4.6% at 4 weeks of age to 1.9% at 6-weeks ($P < 0.05$) (Table 2). For the latter, only structural lipids may have remained, given that the fat content of dead, abandoned newborns was similar at 1.2% (Table 2). In addition, growth rate of CAH calves from 4 to 6 weeks (306 g/d) was lower than that from 0 to 4 weeks (402 g/d) or 6 to 15 weeks (374 g/d) (Table 1).

A midsummer reduction in the rates of weight gain and fattening of calves could result from insect harassment or metabolic weaning (Lavigueur and Barrette 1992). Insects might affect calves both directly, through increased energy expenditure and decreased nursing/feeding time (White *et al.* 1975; Reimers 1980, 1983; Dau 1986), and indirectly, through decreased milk production of their dams due to energy and nutrient imbalance (White 1992; Chan-McLeod *et al.* 1994). The net result may be lower body weights of calves in autumn (Helle and Tarvainen 1984). Also, calves become increasingly independent nutritionally after ca. 40 d of age, as indicated by milk intake (White and Luick 1984; Parker *et al.* 1990) and suckling rate (Parker *et al.* 1990; Lavigueur and Barrette 1992); and therefore may be unable to sustain high growth rates. In fact, milk nutrients may be critical to maximizing growth during midsummer, since they are assimilated more efficiently than those derived from the diet and rumen metabolism (White 1992).

In addition to the effects of insect harassment, poor autumn condition may reflect summer nutrient limitation through habitat degradation (e.g., George River Herd: Messier *et al.* 1988; Huot 1989; Couterier *et al.* 1990; Crête and Huot 1993). Although the Arctic Coastal Plain that constitutes the summer range of the CAH was moderately productive for caribou in the 1970's (White *et al.* 1975; White and Trudell 1980), no recent appraisal

exists. It is noteworthy, however, that calf production has declined steadily over the last decade (Cameron 1995), suggesting food limitation and a resultant increase in the frequency of breeding pauses (Cameron 1994). In addition, the CAH has been exposed to increasing petroleum development on its summer range for > 20 years. Conflicts with various structures and related disturbances (Smith and Cameron 1985a; Smith and Cameron 1985b; Smith *et al.* 1994) could increase the energy costs associated with insect harassment (Cameron 1983), and modify patterns of range use (Smith and Cameron 1983; Cameron *et al.* 1995), thus exacerbating any nutrient shortages.

While inadequate summer nutrition suppresses fecundity among lactating females (see above) and growth of calves (Reimers *et al.* 1983), winter undernutrition reduces birth weights (Rognmo *et al.* 1983; Skogland 1984) and early calf survival (Rognmo *et al.* 1983; Skogland 1990). A decline in overwinter body condition generally is associated with dietary energy limitation (Reimers and Ringberg 1983; Adamczewski *et al.* 1987a), although protein deficiency may also be involved (Huot 1989; Couterier *et al.* 1990). I suggest that CAH females were precariously near protein and energy limitation in 1989-90. Apparently, productivity of the herd was affected, as the proportion of calves born to radiocollared females in 1990 and surviving >48 h was below average (63:100), unlike calf production in 1992 (72:100) (Cameron, unpubl. data). The frequency with which winter undernutrition occurs in the CAH is not known.

The cycle of fatness for captive reindeer was greater in amplitude than that for arctic caribou and approached the extremes reported for Svalbard reindeer. The hybrid male killed in autumn immediately prior to rut had 82 mm of back fat and a fat content of 18% of IFBW, which is nearly identical to the 83 mm and 22% fat, respectively, reported for Svalbard reindeer males just prior to the rut (Reimers and Ringberg 1983). Large male caribou accumulate about 50% less fat (20 kg, McEwan 1968) than Svalbard or semi-domestic reindeer.

The inverse relation between percentages fat and water is a general association for mammals, which allows fat content to be estimated from body water content (e.g. Pace and Rathburn 1945; Reid *et al.* 1968). The slope of that relationship for arctic caribou (-1.125) is less than that reported for Svalbard reindeer (-1.50, Reimers *et al.* 1982) but is within the range for domestic animals (sheep and goats, -1.25, Panaretto 1963; pigs, -1.110 and cattle, -1.118, Reid *et al.* 1968). Mean water content of the fat-free, ingesta-free body for caribou was 68.6 % for adults and 77.6 % for calves < 1 week of age; values for older calves were intermediate. These values agree closely with the mean of 73.2 % water at 0% fat content for guinea-pigs, rabbits, cats and dogs (Pace and Rathburn 1945), suggesting a broad mammalian constant.

Organs as nutrient reserves

Seasonal changes in organ weights may reflect variable metabolic demands. Differences in weights of metabolically active organs have been related to energy expenditure (Mitchell *et al.* 1976; Koong *et al.* 1985), and GI hypertrophy in lactating rats allows maintenance of digestive efficiency while increasing food intake (Campbell and Fell 1964). Weight increases of liver, kidneys, GI tract, and heart during summer and autumn have been previously reported for red deer (Mitchell *et al.* 1976) and caribou (Dauphiné 1975; Adamczewski *et al.* 1987a), but I show that hypertrophy of kidneys and liver were appreciably greater than that of the heart (Fig. 4). This dramatic seasonal phenomena is apparently an adaptation to meet metabolic demands above those of activity, particularly lactation which, in July, exacts a four-fold increase in metabolic demand relative to winter maintenance (White 1992). Liver and kidney hypertrophy is ostensibly not related to detoxification of secondary compounds. Forages high in such compounds were unavailable to captive reindeer, yet they responded similarly to caribou.

A summer increase in heart weight is consistent with higher anabolic demands but also may be associated with greater physical activity (Klafs and Arnheim 1981). The greater increase in heart weight per unit BW for caribou than for reindeer (Fig. 5) is likely due to a difference in activity levels. Daily movements of caribou can be extensive (Fancy *et al.* 1989), generally exceeding those of reindeer held in captivity (White, pers. obs.). It is noteworthy that heart weights for the relatively sedentary Svalbard reindeer averaged 0.6% and 0.7% of BW in summer and winter, respectively, even less than those reported here (0.94% of BW) or for lean captive reindeer (1.0% of BW, Ringberg *et al.* 1981).

In addition to being a response to metabolic demands, tissue hypertrophy in summer constitutes a potential protein reserve. A 50% decrease of kidney and liver weights between July and May represents mobilization of approximately 300 g protein, while halving the tissue of the gastro-intestinal tract releases an additional 750 g protein. The combined weight decreases in these 3 organs could account for all protein lost from the viscera between October and May (Table 4), which represents at least 18% of the total protein loss. Thus, skeletal muscle supplies most (ca. 80%) of the maternal protein mobilized for maintenance and fetal development in winter.

Management Implications

The strong allometric relations between chemical body composition and BW, IFBW, and CW (Fig. 3; Table 3) suggest that these latter weights should provide reliable predictors of body composition in *Rangifer*. Similar models have been reported for white-tailed deer (Robbins *et al.* 1974) and reindeer (Reimers *et al.* 1982). Variability in mathematical relations between chemical composition and IFBW appears to result primarily from differences in rate and degree of fattening, which, in turn, may be partially related to body size and fatness at chemical maturity (e.g., cattle, Berg and Butterfield 1976). As proposed by Moulton (1923), the allometric relations between chemical

composition and fat-free, IFBW appear to be conserved during evolution, as they are virtually identical for Svalbard reindeer, semi-domestic reindeer, and arctic caribou (Fig. 6), even though Svalbard reindeer deposit the most fat per unit decrease in body water (Reimers *et al.* 1982).

Although IFBW is the most precise predictor of chemical composition, it is the most time-consuming of the 3 measurements. BW or CW, on the other hand, can be determined easily in the field. Discretion must be used when applying any such equations, however, since prolonged undernutrition followed by refeeding has been shown to disturb the homeostatic relations between chemical composition and IFBW (Reid *et al.* 1968). In addition, BW may be a weak predictor of body condition if alimentary fill varies excessively (Cameron 1972; Adamczewski *et al.* 1987a).

Finally, weights of internal organs such as the liver and kidneys may be useful indicators of metabolic activity or recent nutrition, particularly when expressed relative to heart weight. In birds, patterns of residuals of the relations between basal metabolic rate (BMR) and BW have been correlated with organ weights, and were related to differences in daily energy expenditure and BMR (Daan *et al.* 1990). Thus organ weights were better predictors of BMR than was BW. Interrelationships between organ size and metabolic rate warrant further study as tools for management.

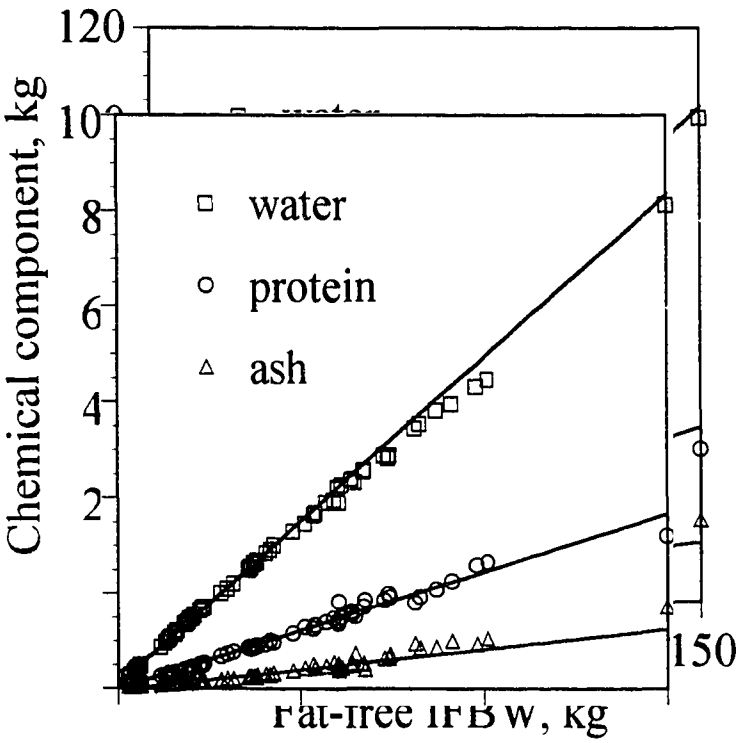

Figure 6. Conservation of fat-free body composition in the genus *Rangifer*. Relations between weights of chemical components and fat-free, ingesta-free body weight (IFBW) in caribou and reindeer. Regression lines are for Svalbard and semi-domestic reindeer (Reimers *et al.* 1982), and data points (and second set of equations, below) are for arctic caribou and semi-domestic reindeer (this study).

Water = 0.166 + 0.690X; or 1.136 + 0.654X, $R^2 = 0.998$.

Protein = -0.082 + 0.239X; or -0.345 + 0.246X, $R^2 = 0.986$.

Fat = -0.084 + 0.071X; or -0.791 + 0.100X, $R^2 = 0.942$.

CHAPTER 2: ESTIMATING FAT CONTENT OF CARIBOU FROM BODY CONDITION SCORES[1]

Abstract: Body condition scores provide a subjective measure of body fatness. I scored the condition of 64 barren-ground caribou and 10 reindeer, which were subsequently killed and analyzed for chemical composition. A body reserve index (the product of body condition score and body weight) was superior to either body weight or body condition score as a predictor of fatness for calves and adults. The probability of pregnancy for 107 adult female caribou was significantly related to both body condition score ($P = 0.017$) and body reserve index ($P = 0.007$).

Introduction

Body condition scoring provides an estimate of the amount of energy stored as fat and muscle. Subjective scoring is a quick, reliable means of identifying extremes of condition, and has been correlated with objective measures of fat and protein content for cattle (Edmonson *et al.* 1989) and sheep (Russell *et al.* 1969). Such scoring systems also have been used in livestock to investigate the effects of fatness on reproductive performance (e.g., Rhind *et al.* 1989).

Body condition indices are based on palpation (Russell *et al.* 1969) or visual scoring (Edmonson *et al.* 1989). Visual scoring of barren-ground caribou (*Rangifer tarandus granti*) and reindeer (*R. t. tarandus*) is not possible during most of the year because a dense hair coat prevents evaluation of body contours. Therefore, I used palpation to assess the relative amount of subcutaneous tissue. The objective was to determine the efficacy of the body condition score (BCS) and body weight (BW) to

[1]Gerhart, K.L., White, R.G., Cameron, R.D., and Russell, D.E. Submitted. Estimating fat content of caribou from body condition scores. J. Wildl. Manage. **00**: 00-00.

predict fatness and, in turn, pregnancy status of caribou. Preliminary results have been published previously (Gerhart *et al.* 1992).

Methods

Fifteen adult female caribou of the Central Arctic Herd, and 37 Central Arctic and 12 Porcupine Herd calves ranging in age from 1 to 134 d were shot from a helicopter, weighed to the nearest 0.5 kg, and scored for body condition. Also weighed, scored, and killed (with a captive bolt-gun) were 9 adult male reindeer and 1 adult male caribou/reindeer hybrid that were pen-fed at the Large Animal Research Station, Institute of Arctic Biology, to achieve a wide range of fatness. The BCS was based on palpation, and was determined as the sum of subjective ratings from 1 to 5 (1 = emaciated, 5 = obese) of the amount of soft tissue at each of 3 sites: withers, ribs, and rump (Table 5). The product of BW and BCS was termed the body reserve index (BRI). Fat content of the ingesta-free body was determined by petroleum ether extraction (Chapter 1) and is presented here as a weight (kg) or as a percentage of the ingesta-free body weight. Relations between fat content and the variables BW, BCS, and BRI were determined using analysis of variance for unbalanced data (GLM in SAS) and linear regression (SAS). Data for BW and BRI were logarithmically-transformed.

An additional 107 adult female caribou of the Porcupine Herd were captured in early- to mid-November 1990-1992 by helicopter using a net gun or a dart (1.0 mg carfentanil/100 kg), and weighed and scored as part of a separate study (Chapter 3). Blood samples were drawn by jugular venipuncture, and pregnancy status was determined from plasma progesterone concentration (Niswender 1973). Females with > 1.5 ng progesterone / ml plasma were classified as pregnant (Russell, unpubl. data). Relations between pregnancy probability and both BCS and BRI were determined using logistic regression (BMDP).

Table 5. Descriptive criteria of the body condition score for caribou and reindeer.

	Region of body		
Score	Withers (shoulders)	Ribs	Base of tail[1], hips
5 (Obese)	• Top forms broad, inverted "U"	• Not discernible	• Spine not discernible
4	• More "V" shaped	• Discernible toward abdomen only	• Top of the spine discernible, sides are not
3	• "V" shaped bones easily discernible at top • Slight posterior depression	• Easily discernible • Depressions between ribs less than width	• Top easily discernible, sides partially covered
2	• Bone and connective tissue easily discernible at edge of scapulae • Pronounced posterior depression	• Distinct depressions between ribs • Fleshy regions behind shoulders	• Tops and sides of spine discernible • Point of hips discernible
1 (Emaciated)	• Skin and connective tissue only on top	• Depressions between ribs equal to width	• Individual vertebrate discernible • Points of hips protrude

[1] 5-7 cm anterior to base of tail

Results

Using BCS, I was able to distinguish extremely lean calves (<2 % fat) from others (Table 6). However, even though BCS tended to increase with fat content, differences in BCS were not significant for calves having > 2 % fat. For adults, distinguishing between thin (<4 % fat) and fat (>8% fat) individuals was possible using either BCS or BRI; means of both indices increased with fatness, independent of BW.

BRI was superior to both BW and BCS as a predictor of fatness for adults and older (>100 d) caribou calves (Figure 7). In addition, probability of pregnancy was significantly related to both BCS and BRI for Porcupine Herd caribou (Figure 8).

Discussion

A useful predictor of fatness should be applicable over the entire range of body condition for the study population, and its predictive ability should be superior to that of BW alone (Reid *et al.* 1968), else BW may be preferred. However, BW of ruminants is a relatively unreliable predictor of body fat content because of unknown changes of alimentary fill (e.g., Reid *et al.* 1968). Also, for lean caribou, BW tends to stabilize despite continued mobilization of fat stores (Dauphiné 1971), thereby decreasing reliability.

The strong relation between fatness and both BCS and BRI may be related in part to the ease with which subcutaneous fat depots can be palpated. For obese caribou and reindeer, the largest fat depot is subcutaneous (Reimers and Ringberg 1983; Pond *et al.* 1993). Moreover, the relation between total dissectable fat and depth of back fat is linear or near-linear in *Rangifer* (Reimers and Ringberg 1983; Adamczewski *et al.* 1987b; Pond *et al.* 1993), permitting the use of back fat indices to estimate total body fat.

Table 6. Comparison of body condition indices at various levels of fatness. Mean (± 1 SE) fat content, body condition score (BCS), body weight (BW), and body reserve index (BRI = BCS * BW) for calf caribou, adult caribou, and reindeer categorized by body fat content (% ingesta-free body weight).

AGE	% fat	BCS	BW, kg	BRI	n
Calves	< 2.0	6.6 ± 0.6^{a}	11.9 ± 2.5^{a}	90 ± 23^{a}	11
(< 140 d)	2.0 - 3.9	$7.4 \pm 0.2^{b,c}$	16.7 ± 2.5^{a}	$135 \pm 19^{a,b}$	20
	4.0 - 5.9	$7.7 \pm 0.2^{a,c}$	29.6 ± 5.2^{b}	222 ± 35^{b}	9
	≥ 6.0	$7.9 \pm 0.1^{a,c}$	$44.3 \pm 3.7^{b,c}$	350 ± 29^{c}	9
Adults	<4.0	4.9 ± 0.4^{a}	78.7 ± 3.4^{a}	386 ± 31^{a}	8
(>1.5 y)	4.0 - 5.9	$6.6 \pm 0.7^{a,c}$	81.4 ± 4.5^{a}	545 ± 80^{a}	5
	6.0 - 7.9	$7.6 \pm 0.6^{a,c}$	80.7 ± 6.7^{a}	627 ± 100^{a}	4
	8.0 - 14.9	$9.9 \pm 1.2^{b,c}$	106.1 ± 11.2^{b}	$1011 \pm 65^{a,c}$	4
	≥ 15.0	11.0 ± 1.3^{b}	$147.3 \pm 21.4^{b,c}$	$1703 \pm 486^{b,c}$	4

Note: Means within a column with different letters are significantly different.

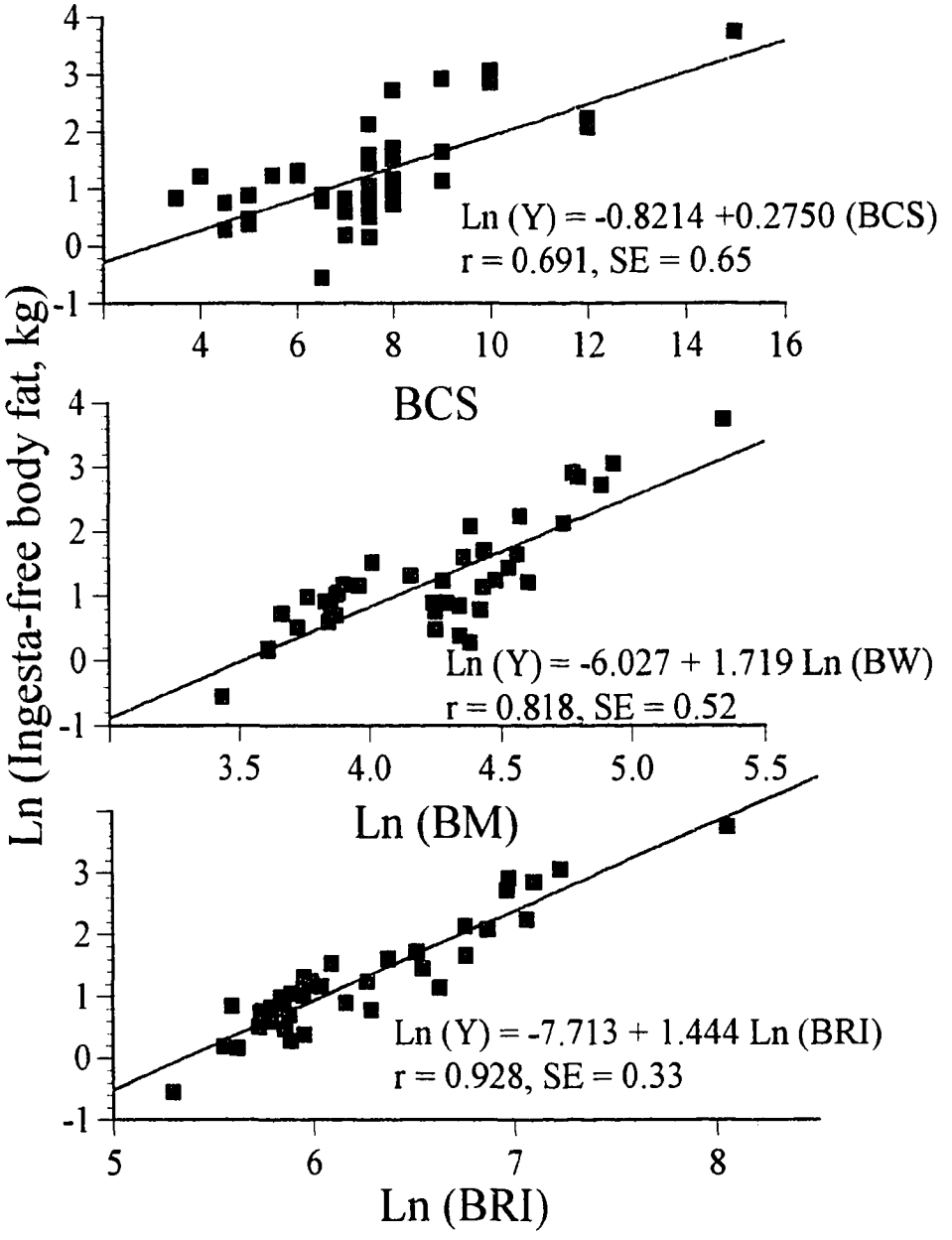

Figure 7. Prediction of body fat from body condition indices. Relation of ingesta-free body fat (kg) to body condition score (BCS), body weight (BW) and the body reserve index (BRI = BCS * BW) for caribou calves in autumn and for adult caribou and reindeer. Logarithmic relations are base e.

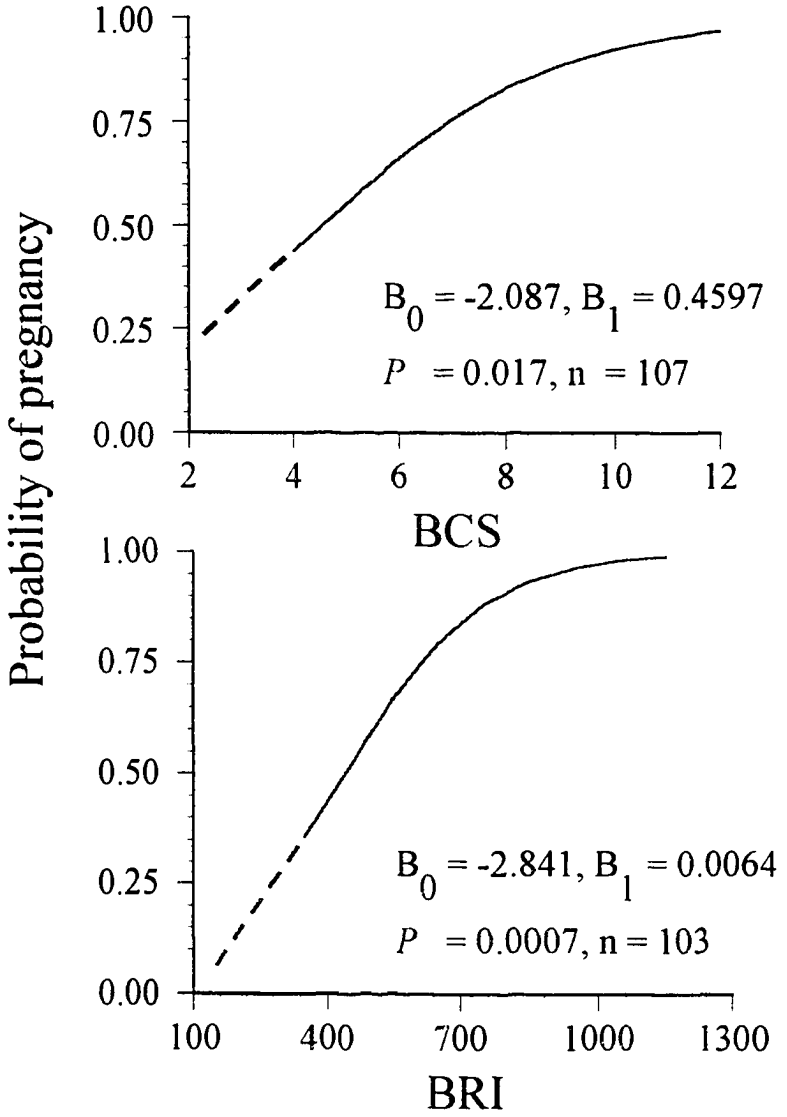

Figure 8. Relation between probability of pregnancy and body condition indices. The logistic relations between probability of pregnancy and both body condition score (BCS) and body reserve index (BRI = BCS * body weight) for adult female caribou of the Porcupine Herd. Dashed lines represent extrapolations beyond the range of data.

Visceral, intermuscular and intramuscular fat depots were not palpable. Although relatively small amounts of fat are deposited intermuscularly (Adamczewski *et al.* 1987b; Pond *et al.* 1993), changes in visceral and intramuscular fat depots can be substantial (Adamczewski *et al.* 1987b; Pond *et al.* 1993). Moreover, caribou with less than 1.5 kg dissectable fat (Adamczewski *et al.* 1987b), or <6 % chemically extractable fat (Huot and Goudrealt 1985), generally have no back fat. In spite of these non-palpable fat reserves and the early mobilization of back fat, both BCS and BRI were useful predictors of fatness over the range examined. Extreme leanness of caribou and reindeer (<4% fat) was detectable, as was the presence and relative amount of fat (6 -18 % fat). In addition, BCSs were better estimators of fatness than BW alone (Fig. 7).

BCS was less useful as a predictor of fatness for growing calves, ostensibly because they deposit little fat subcutaneously. Rather, fat deposition is primarily visceral, intermuscular, and intramuscular. Indeed, calves are typically lean (≤ 7% fat, Reimers *et al.* 1981, Ringberg *et al.* 1981; Chapter 1), and the allometric relations between chemical composition and BW or IFBW are relatively invariable (Chapter 1). Therefore, BW is a better predictor of fatness in calves than it is in adults. Calves of the Central Arctic and Porcupine herds begin to deposit back-fat at approximately 100 d of age, when lean growth pauses for the winter (Gerhart *et al.* 1995; Chapter 4). For these calves, BCS and BRI are superior to BW as predictors of fatness.

For adult female caribou in autumn, both BCS and BRI are directly related to probability of pregnancy (Fig. 8), as is BW (Cameron *et al.* 1993). BCS, in particular, may prove useful in assessing condition when BW determinations are impractical.

Although BCS involves an element of subjectivity, errors are not necessarily serious. Scoring systems often yield repeatable results, independent of assessors' experience (Edmonson *et al.* 1989). Therefore, subjectivity alone does not preclude the use of BCS in field situations.

CHAPTER 3: PREGNANCY OF ADULT CARIBOU: EVIDENCE FOR LACTATIONAL INFERTILITY[1]

Abstract: To examine the relations between pregnancy, body condition, and lactation, 106 adult female caribou (*Rangifer tarandus granti*) of the Porcupine Herd were captured, weighed, measured, and scored for body condition in November 1990-1992. Blood samples were drawn for determination of pregnancy, and body fat content (kg) was estimated from the product of body weight and the body-condition score. Pregnant females were significantly fatter and heavier than nonpregnant females, and nonlactating females were significantly fatter, but no heavier than lactating caribou. Probability of pregnancy was positively correlated with body weight and fat content, but prediction of pregnancy was improved when multiple independent variables, including skeletal dimensions and lactation status, were included in logistic models. Nonlactating females were more fertile than lactating females at a particular body weight and metatarsus length; but, at the same fatness, they were not more fertile than females that had lactated through summer and were ceasing lactation in November. However, females that were extending lactation in November were least fertile, and this reduction of fertility was not explained by differences in body condition or skeletal dimensions. I suggest that the extended lactation group is exhibiting lactational infertility. Finally, unexplained differences in the relation between pregnancy rate and body condition exist among years, suggesting that interannual patterns in the nutrition and ecology of caribou affect the physiological relation between pregnancy and body condition.

[1]Gerhart, K.L., Russell, D.E., Wetering, D., White, R.G. and Cameron, R.D. In Prep. Pregnancy of caribou: Evidence for lactational infertility. J. Zool. Lond. **00:** 00-00.

Introduction

In long-lived animals, reproductive output reflects a trade-off between maximizing production and survival of current offspring and accruing sufficient resources to survive and reproduce again (Trivers 1974; Clutton-Brock and Godfray 1991). An individual's success in meeting these competing needs determines its lifetime reproductive output. Arctic caribou must partition resources to meet the conflicting nutritional demands of lactation and replenishment of maternal body reserves during the brief nutrient pulse of the arctic summer. Failure to provide sufficient milk may slow calf growth (Loudon *et al.* 1983; Loudon and Kay 1984; White and Luick 1984) and therefore threaten calf survival overwinter (Haukioja and Salovaara 1978; Clutton-Brock *et al.* 1985), while failure to replenish maternal fat and protein depots may reduce the female's own subsequent reproductive success (see below) or survival (Albon *et al.* 1983; Clutton-Brock *et al.* 1983).

Fertility of female mammals is correlated with body size and body composition. Previous studies indicate that a female must accumulate a critical amount of fat (Sadlier 1969; Frisch *et al.* 1973), reach a critical body weight (Kennedy and Mitra 1963; Frisch and Revelle 1970; Smith 1991), or achieve a minimum fat:lean ratio (Frisch and McArthur 1974) to achieve puberty or maintain ovulation. Otherwise, an annually-breeding female must reduce the number of offspring produced, or for nulliparous species, forego reproduction for that year.

Reproductive data from *Rangifer tarandus* subspecies support the hypothesis that a critical body fat level or body weight must be reached for a female to conceive. Pregnant barren-ground caribou (*R.t. groenlandicus* and *R.t. granti*) were fatter in early winter than nonpregnant females (Dauphiné 1976; Allaye-Chan 1991) and wild Norwegian reindeer (*R. t. tarandus*) with heavier autumn carcass weights were more likely to be pregnant (Reimers 1982). Pregnancy status for Peary caribou (*R.t. pearyi*) in late winter

was highly correlated with both body weight and indices of body fat (Thomas 1982). Most recently, parturition rate for Alaska barren-ground caribou (*R. t. granti*) has been correlated with autumn body weight (Cameron *et al.* 1993; Cameron and Ver Hoef 1994), and a body-fat threshold for ovulation has been reported for woodland caribou (*R.t. caribou*; Crête *et al.* 1993).

In addition to the role of body condition, lactation may cause infertility in cervids (Mitchell and Brown 1974; Loudon *et al.* 1983; Albon *et al.* 1986), as for humans (Bongaarts 1980). Lactational infertility for seasonally breeding animals is apparently mediated by plane of nutrition (Loudon *et al.* 1983), while the role of nutrition in maintaining lactational amenorrhea for humans is contested (Bongaarts 1982; Frisch 1982). Rather than reducing the body condition of the female, lactation may cause infertility primarily through increased suckling frequency of the offspring (Loudon *et al.* 1983).

I examined pregnancy status of caribou in relation to both body condition and previous reproduction. The objectives were: (1) to determine whether a critical body weight or fatness for pregnancy exists for caribou; (2) to determine the effect of lactation on probability of pregnancy; and (3) to develop a model for predicting pregnancy of caribou that is suitable for management applications.

Methods

In November 1990-92, 106 adult female caribou (*R. t. granti*) of the Porcupine Herd were captured from a helicopter (Bell 206B) with either a Marley net gun (1990 and 1992) or a Cap-chure dart gun (1991; 1.0 mg/100 kg carfentanil, and 200 mg of its antagonist, naloxone). Blood samples were drawn by jugular venipuncture, presence of a calf at heel and milk in the mammary were noted, and milk samples were collected (where appropriate). Body weight (nearest 0.5 kg), a body-condition score (a sum of indices

ranked from 1 (low) to 5 (high) of soft tissue covering bone at 3 sites on the animal; Gerhart *et al.* 1992; Chapter 2), and mandible and metatarsus lengths (mm) were recorded. Pregnancy was determined from plasma progesterone concentration (Niswender 1973). Females with a progesterone concentration of >1.5 ng/ml were pregnant (Figure 9; Russell In prep).

In 1990, a front incisor was removed for age determination (Matson 1981), while in 1992 age was determined from tooth wear. Caribou were not aged in 1991. Females with 2-4 cementum rings (P. Merchant, Yukon Territories Government) or with little or no tooth wear were classified as "young", those having 5-10 cementum rings or moderate tooth wear were classified as "intermediate" in age, and those with >10 cementum rings or with heavily worn teeth were considered "old". Ages were not estimated for 32 females. No yearlings (identified by facial structure and lanky conformation) were included in this study.

Lactation class was based on characteristics of the milk and udder. Females with contracted udders containing no fluid or a small volume of clear fluid were considered nonlactating. The nonlactating class included both females that were not pregnant during the previous winter and those that were pregnant but lost their calves during the summer. Lactating females were classified according to milk composition (White *et al.* In prep): females with ≤2 % lactose (wet-weight) in early November were defined as ceasing lactation, while those with >2% lactose were classified as extending lactation.

Body composition was estimated using previously validated prediction equations derived from caribou and reindeer. Fat content (kg, dry weight) was estimated by solving a logarithmic equation relating body fat to the product of body weight and body-condition score, and taking the antilog :

$$[1]\quad \text{Log}_e(\text{fat}) = -7.713 + 1.444*\text{Log}_e(\text{BW}*\text{BCS})$$

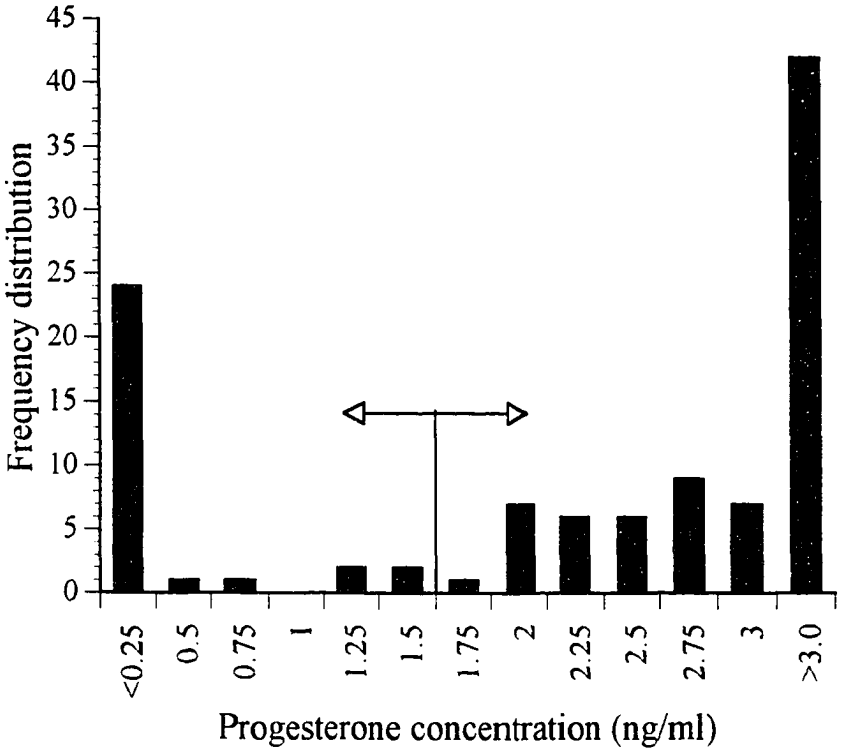

Figure 9. Relation between pregnancy and plasma progesterone levels in caribou 2-4 weeks after the breeding season. Frequency distribution of plasma progesterone levels among adult female caribou of the Porcupine Herd in November 1990-1992. Females with plasma progesterone concentrations greater than 1.5 ng/ml were considered pregnant (Russell *et al.* In Prep.).

($R^2 = 0.86$, $P<0.0001$, SE of $Log_e(Y) = 0.34$; Chapter 2).

Body protein content (kg, dry weight) was estimated similarly from a logarithmic equation relating protein and body weight:

$$[2]\ Log_e(protein) = -1.8051 + 1.033 * Log_e(BW)$$

($R^2 = 0.99$, $P < 0.0001$, SE of $Log_e(Y) = 0.034$; Chapter 1)

Relations between variables (and interaction terms, where appropriate) were evaluated using the analysis of variance procedure for unbalanced data (GLM in SAS, 1982). Differences between proportions were examined using the likelihood ratio Chi-square. Mathematical models relating pregnancy to independent variables (body weight, body fat and protein, skeletal measurements, year, lactation, and age class) were described using stepwise logistic regression (BMDP) based on binary data:

$$[3]\ \Pi(x) = e^{g(x)}/(1 + e^{g(x)})$$

where $g(x) = \beta_n + \beta_1 X_1 + ... + \beta_n X_n$, and $\Pi(x)$ is the probability of pregnancy at a particular $X_1, X_2, ..X_n$ Goodness of fit was tested using the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 1989). Appropriateness of the scale of the logit was assessed according to Hosmer and Lemeshow (1989). The fit of the logit was linear for all continuous variables. Statistical significance was $P<0.05$, except in logistic regression models, where $P<0.1$ was used for inclusion and removal of independent variables.

Results

Body condition

Body condition of female caribou differed among pregnancy and lactation classes (Table 7). Pregnant caribou were heavier and fatter than their nonpregnant counterparts, and nonlactating females were fatter than lactating ones. Body fat content and body

Table 7. Chemical composition of female caribou in November. Mean body weight (BW), body composition and skeletal dimensions (± 1 SE) of adult female caribou of the Porcupine Herd, categorized by pregnancy status, lactation class, age, and year of capture.

Group	n	BW, (kg)	Fat, (kg)	Protein, (kg)	Mandible, (cm)	Metatarsus, (cm)	% Preg
Pregnancy status							
Pregnant	78	91.4 ± 1.0^a	5.6 ± 0.2^a	17.5 ± 0.2^a	27.4 ± 0.1^a	39.5 ± 0.1^a	
Nonpregnant	24	86.4 ± 1.8^b	4.3 ± 0.3^b	16.5 ± 0.4^b	27.1 ± 0.2^a	39.7 ± 0.1^a	
Lactation Class							
Nonlactating	26	91.2 ± 2.0^a	6.4 ± 0.6^a	17.4 ± 0.4^a	27.1 ± 0.2^a	39.5 ± 0.2^a	89.3^a
Weaning	48	89.7 ± 1.2^a	5.0 ± 0.2^b	17.1 ± 0.2^a	27.3 ± 0.2^a	39.4 ± 0.1^a	87.8^a
Extended Lactation	28	90.2 ± 1.5^a	4.7 ± 0.3^b	17.2 ± 0.3^a	27.4 ± 0.2^a	39.8 ± 0.1^a	48.3^b
Lactation and Pregnancy status							
Nonlactating Pregnant	23	93.1 ± 2.1^a	6.6 ± 0.4^a	17.8 ± 0.4^a	27.4 ± 0.2^a	39.5 ± 0.2^a	
Lactating Pregnant	55	90.7 ± 1.1^b	4.3 ± 0.3^a	17.3 ± 0.2^a	27.4 ± 0.1^a	39.5 ± 0.1^a	
Lactating Nonpregnant	21	87.8 ± 1.9^b	5.1 ± 0.2^a	16.8 ± 0.4^a	27.3 ± 0.3^a	39.7 ± 0.2^a	

Table 7 (continued)

Age class*							
Young	35	83.4 ± 1.0^{a}	4.6 ± 0.2^{a}	15.9 ± 0.2^{a}	26.7 ± 0.2^{a}	39.3 ± 0.2^{a}	68.6^{a}
Intermediate	33	91.9 ± 1.1^{b}	5.0 ± 0.3^{a}	17.6 ± 0.2^{b}	27.7 ± 0.1^{b}	39.8 ± 0.1^{a}	84.9^{a}
Old	6	94.3 ± 1.9^{b}	5.1 ± 0.1^{a}	18.0 ± 0.4^{b}	27.7 ± 0.4^{b}	40.1 ± 0.4^{a}	83.3^{a}
Year							
1990	60	88.0 ± 1.0^{a}	4.7 ± 0.2^{a}	16.8 ± 0.2^{a}	27.4 ± 0.1^{a}	39.6 ± 0.1^{a}	78.3^{a}
1991	21	$99.4 \pm 1.7^{b**}$	$7.2 \pm 0.5^{b**}$	$19.0 \pm 0.3^{b**}$	27.3 ± 0.3^{a}	39.2 ± 0.2^{a}	80.0^{a}
1992	25	89.3 ± 1.5^{a}	5.3 ± 0.2^{a}	17.1 ± 0.3^{a}	27.1 ± 0.2^{a}	39.6 ± 0.2^{a}	76.0^{a}

Note: Means and SE's with different superscripts within a group and column are significantly different ($P < 0.05$)

*Young, 2-4 cementum rings or little tooth wear; intermediate, 5-10 rings or moderate tooth wear; old, >10 rings or heavily worn teeth.

**n=17

weight did not differ between females that were ceasing and extending lactation, although pregnancy rate was higher among those ceasing lactation ($P < 0.001$). The inter-relationships between pregnancy rate, lactation status and body condition became clearer when caribou were grouped according to both lactation and pregnancy status. All caribou were either lactating or pregnant (or both) except 3 light, skeletally small females.

Age-related differences of body condition and skeletal size were apparent (Table 7), although age class was unrelated to pregnancy ($P = 0.26$). "Young" females had shorter mandibles, lower body weights, and less body protein than did older females. Differences between age classes for body fat content or metatarsus length were not discernible.

Body condition of caribou varied among years. Mean body weight, fat content and protein content were significantly higher in 1991 than in 1990 or 1992 (Table 7). However, pregnancy rate did not increase accordingly, but remained at 76-80%. The proportion of lactating females that were ceasing to produce milk also varied annually, ranging from 79.6% in 1990 to 31.6% in 1992 ($P<0.001$).

Prediction of pregnancy status

Of the body condition variables, body fat content (kg) was the parameter which best explained differences in pregnancy rate in simple logistic regression models. However, fat content (%), fat:protein ratio, and body weight were also good correlates of pregnancy (Table 8). Because of the high degree of colinearity between body protein and body weight, protein and weight were offered separately in subsequent (step-wise) logistic regression models.

The most parsimonious stepwise logistic regression model predicting pregnancy status of caribou consisted of lactation class, body fat content and mandible length (Table 9, model 1). Females that were ceasing lactation or were nonlactating were 40% more

Table 8: Logistic relations for prediction of pregnancy status. Relation between pregnancy status and each independent variable in simple logistic regression estimated using maximum likelihood ratios.

Independent variable	Log-likelihood ratio	Degrees of Freedom	*P*-value
Lactation class	-46.57	2	0.0001
Estimated Body Fat (kg)	-49.76	1	0.0008
Percent Fat	-51.08	1	0.003
Fat:Protein Ratio	-51.16	1	0.004
Body weight (kg)	-51.98	1	0.009
Milk (yes, no)	-53.77	1	0.07
Mandible length (cm)	-54.47	1	0.18
Metatarsus length (cm)	-54.93	1	0.34
Year (1990&1992 vs. 1991)	-55.21	1	0.56
Percent Protein	-55.38	1	0.99

Note: *P* is the probability that $\beta = 0$ for each independent variable when no other variables have entered the regression.

Table 9: Equations predicting probability of pregnancy. Parameter estimates from stepwise logistic regression models describing the relationships between pregnancy status, body composition, lactation status, and skeletal measurements (see Figs. 1-3).

Independent variables	Parameter Estimate (β)	Standard error	*P*-value	Percent misclassified
Model 1: All independent variables offered				
Lactation Class[a] (1)	2.241	0.64	0.0003	
(2)	2.095	0.84		
Estimated Body Fat (kg)	0.5764	0.24	0.005	
Mandible length (cm)	0.4905	0.28	0.070	
Constant	-16.31	7.8	0.030	15.8
Model 2: All variables except lactation class offered				
Estimated Body Fat (kg)	0.7345	0.21	0.001	
Year[b] (1991 or '90 & '92)	-1.841	0.82	0.021	
Constant	-2.123	0.97	0.019	18.8
Model 3: All variables except lactation class and fat content offered				
Body weight (kg)	0.153	0.04	0.0001	
Year[b] (1991 or '90&'92)	-2.433	0.89	0.005	
Metatarsus length (cm)	-0.871	0.37	0.01	
Milk[c] (yes, no)	-1.193	0.74	0.08	
Constant	23.43	13.5	0.06	22.8

[a] Extended lactation X(1)=0, X(2)=0; ceasing lactation X(1)=1, X(2)=0; nonlactating X(1)=0, X(2)=1.

[b] 1990 and 1992, X=0; 1991, X=1.

[c] No milk in the udder, X=0; milk in the udder, X=1.

Note: *P* is probability that β=0 for the full model. There is no evidence for lack of fit.

likely to be pregnant at 4 kg body fat and mean mandible length than were females that extended lactation (Figure 10). A 2 cm increase in mandible length correlated with up to a 20% greater likelihood of pregnancy.

Because cessation of lactation can be identified only during a brief period in early winter, the data were then analyzed without differentiating between females that were extending and ceasing lactation. With this adjustment, the most significant predictors of pregnancy were body fat content and year (Table 9, model 2). Data from 1990 and 1992 were combined, since mean fatness and pregnancy rate did not differ between these years; comparison of full (three year classes) and reduced (1990 and 1992 vs. 1991) logistic models verified statistically the acceptance of the reduced model ($\chi^2 = 1.56 < 3.84$, $P<0.05$). Fatter females were more likely to be pregnant, and approximately 2 kg more fat was required in 1991 than in 1990 or 1992 to achieve a 50% probability of pregnancy (Figure 11).

Because fatness has been considered impractical to measure for live caribou, the data were analyzed a final time without estimators of fatness. Body weight, year, metatarsus length, and milk (presence or absence) were significant predictors of pregnancy status (Table 9, model 3). Nonlactating females were significantly more likely to be pregnant than lactating females at a particular body weight and metatarsus length (Figure 12): to achieve a 50% probability of pregnancy, lactating caribou had to weigh 8 kg more than nonlactating females. Nevertheless, between year differences in the relation between body weight and pregnancy affected probability of pregnancy more than did lactation status within a year. For instance, a lactating female in 1991 had to be approximately 16 kg heavier than a 1990 or 1992 lactating female to achieve a 50% probability of pregnancy; the same female had to be 10 kg heavier than a 1991 nonlactating female to achieve a similar pregnancy rate. In addition, a 10 mm difference of metatarsus length

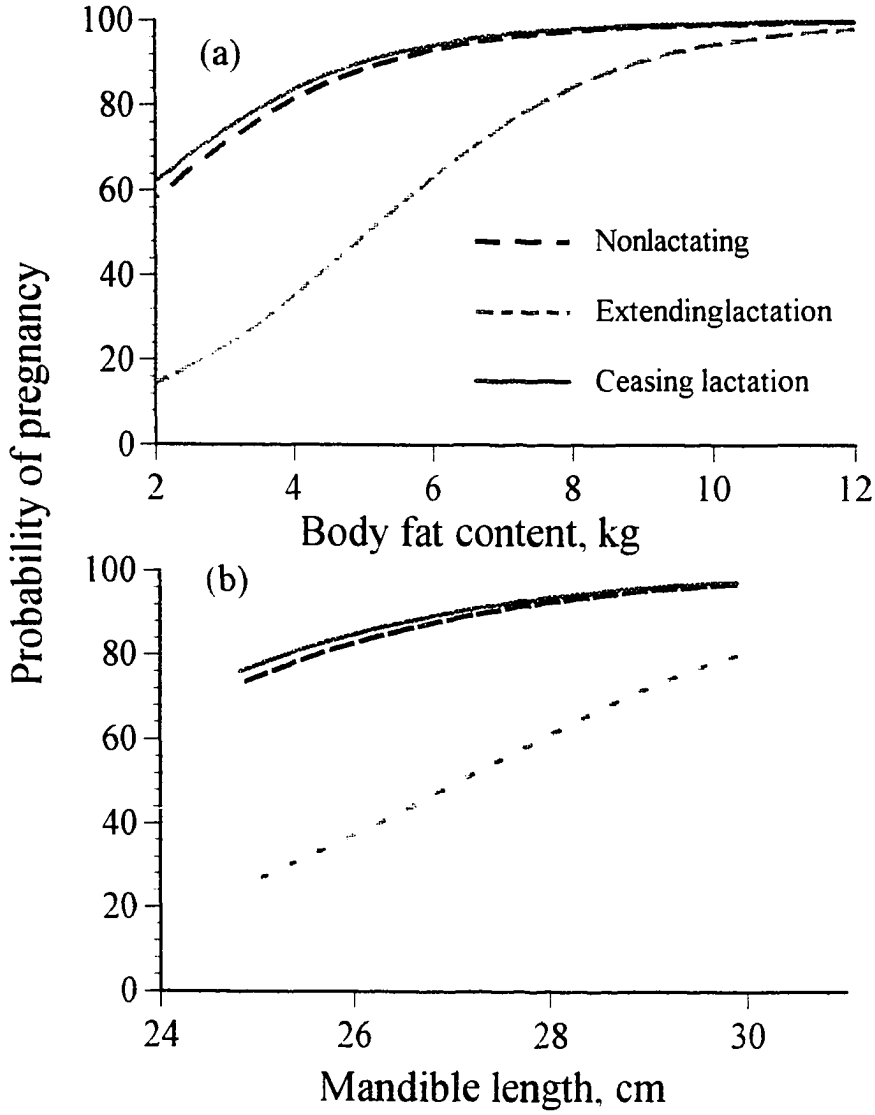

Figure 10. Probability of pregnancy in relation to body fat and lactation class at mean mandible length (a) and in relation to mandible length and lactation class at mean fatness (b) for adult female caribou of the Porcupine Herd (see Table 3, model 1).

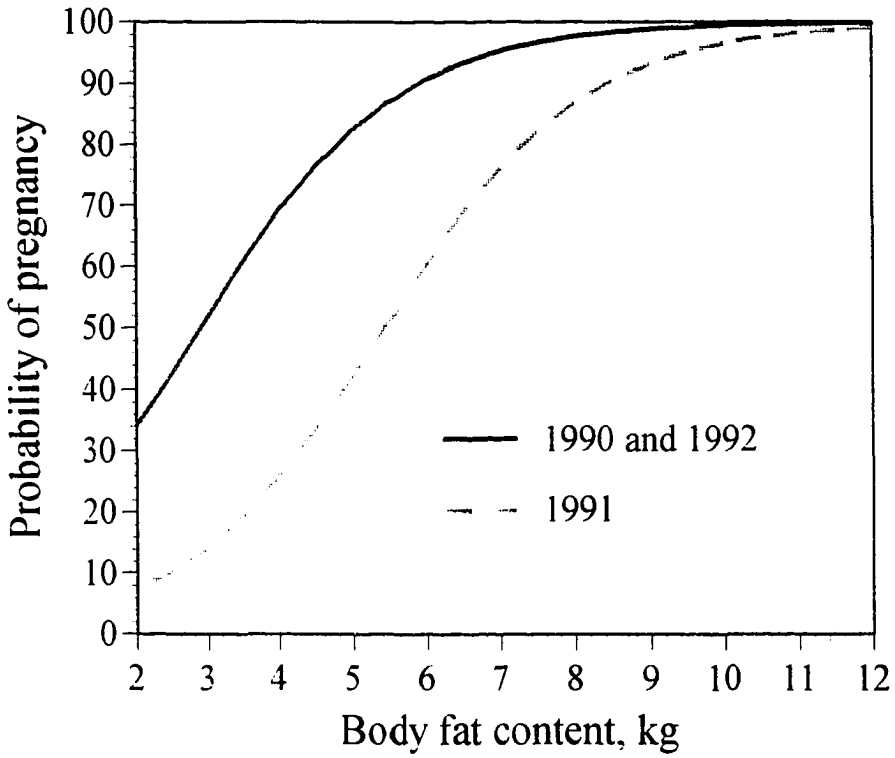

Figure 11. Probability of pregnancy in relation to body fat and year for adult female caribou of the Porcupine Herd (see Table 3, model 2).

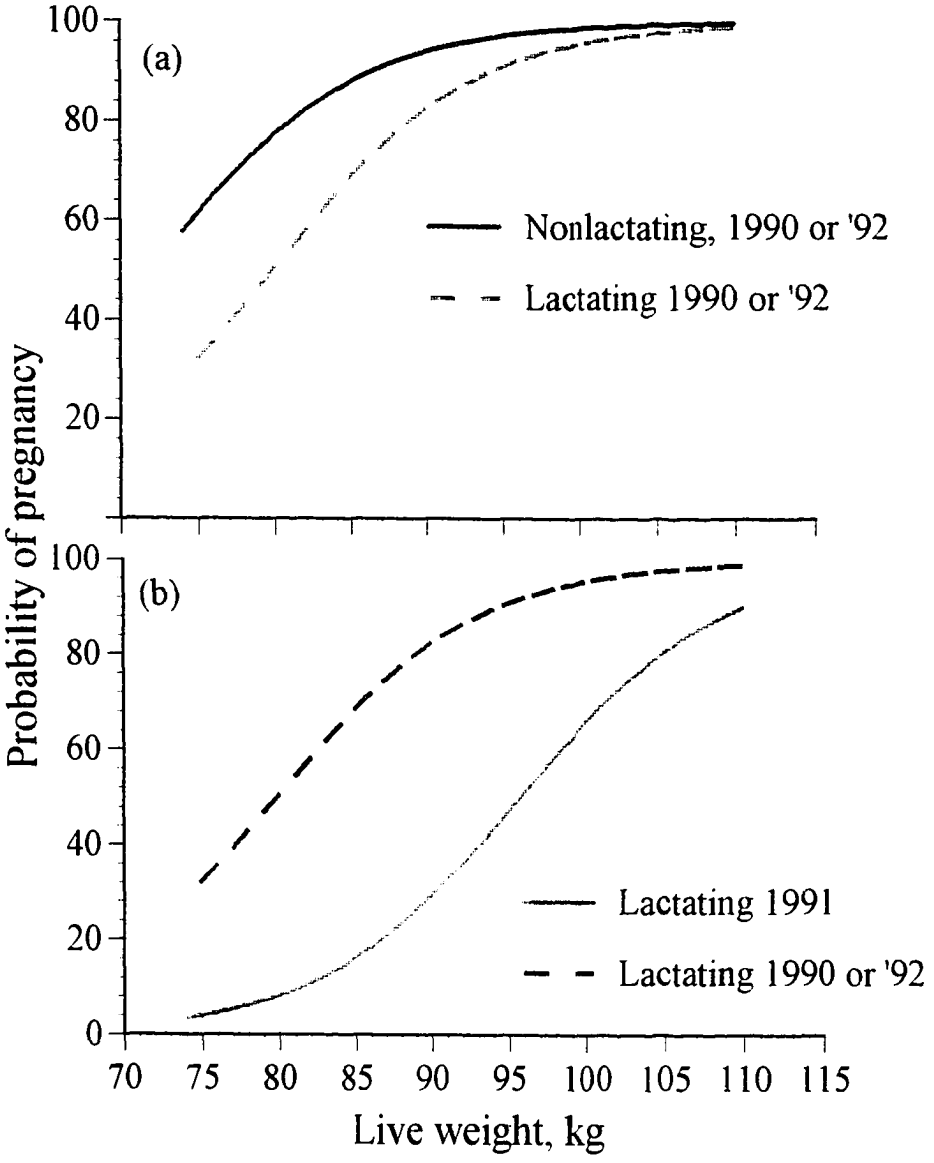

Figure 12. Probability of pregnancy in relation to body weight and year for (a) nonlactating versus lactating caribou in 1990/92 and (b) lactating caribou in 1991 versus 1990/92 (see Table 3, model 3).

between lactating females weighing 87.5 kg correlated with nearly a 20% decrease in probability of pregnancy for the longer-legged female.

Simple logistic regression between pregnancy and body weight produced a curve similar to that reported for Central Arctic Herd caribou (Cameron and Ver Hoef 1994; Figure 13). The relation between pregnancy and body weight for Porcupine Herd caribou, however, varied between years (P=0.08) as described above, whereas that for the Central Arctic Herd did not. In addition, while body weight was a significantly correlate to pregnancy when all classes of females were included, it was not related to pregnancy among lactating females (P=0.5).

Age class did not enter logistic regression models as a predictor of pregnancy. No quadratic or higher terms entered the equations, and interaction terms were either intercorrelated with independent variables or failed to pass significance tests to enter the regression. All 3 models misclassified a similar proportion of females (Table 9), and nonpregnant animals were misclassified most often (56%, 95%, and 80% of misclassified caribou in models 1, 2, and 3, respectively).

Discussion

Relations between pregnancy and body condition

Probability of pregnancy for caribou of the Porcupine Herd varied directly with body condition, as reported previously for other *Rangifer* populations (Dauphiné 1976; Thomas 1982; Reimers 1983; Cameron *et al.* 1993): fatter and heavier females were more likely to be pregnant. Fatness, in turn, was influenced by previous reproduction, as noted for other populations (Dauphiné 1976; Huot 1989; Tyler 1990): nonlactating females were fatter than females that had supported calves until early winter. Body weight and body fat of PCH females did not decline discernibly with age, as noted for some food-limited *Rangifer* populations (Skogland 1984; Tyler 1990); however, age categories in this study were broad, which may have precluded detection of small changes in condition.

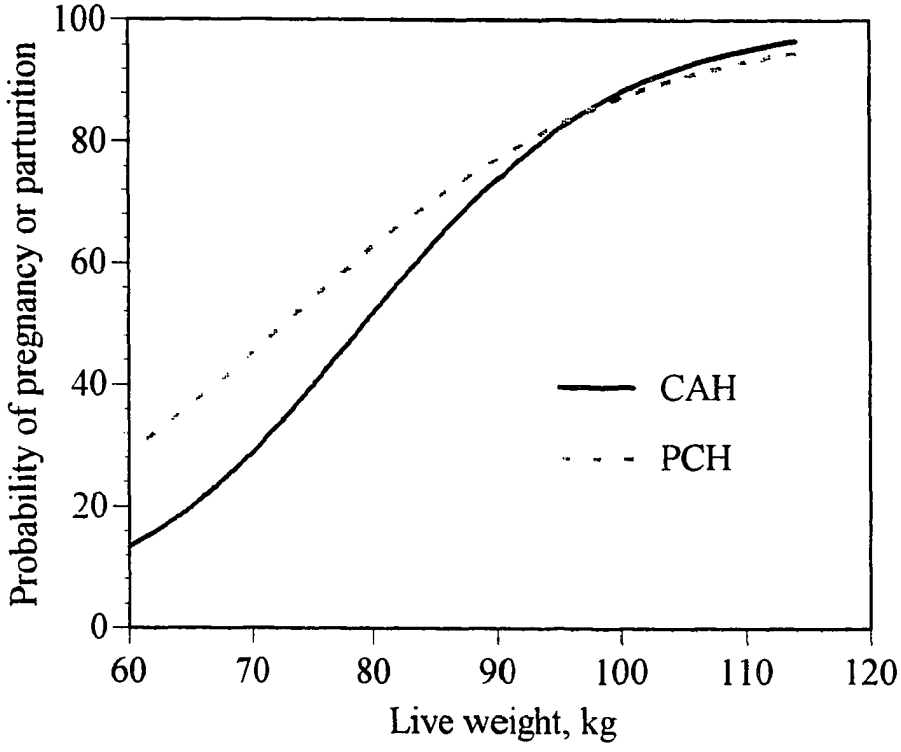

Figure 13. Pregnancy of Central Arctic and Porcupine Herd caribou. Probability of pregnancy in relation to body weight for Porcupine Herd caribou (PCH) and probability of parturition for Central Arctic Herd (CAH) caribou (Cameron and Ver Hoef 1994). Logistic regressions were derived from body weight alone. Values for β_0 and β_1 are -7.69 and 0.097, respectively, for the CAH, and -5.13 and 0.071 for the PCH.

In contrast to previous analyses by Cameron and Ver Hoef (1994), probability of pregnancy of caribou was influenced by indices of frame size. Metatarsus length was inversely related to probability of pregnancy at a particular body weight (model 3), while mandible length was directly related to probability of pregnancy at a particular fatness (model 1). Metatarsus and mandible lengths of individual caribou were very weakly correlated ($R^2 = 0.114$); therefore the two skeletal measurements were not comparable indices of frame size. Growth of metatarsus bones is complete by 2.5 y for barren-ground caribou (Dauphiné 1976), and metatarsus length was not related to age in this study ($P > 0.05$). In contrast, mandibles grow until 5.5 y for caribou (Dauphiné 1976), and mandible lengths of "young" females in this study were shorter than those of older females (Table 7). Growth ceases for female reindeer after initiation of reproduction (Skogland 1983); if the same is true for caribou, mandible length for females is determined by a tradeoff between body growth and reproduction, while metatarsus growth is complete before female arctic caribou begin to reproduce (Dauphiné 1976; Whitten 1991; Cameron *et al.* 1993). Since the growth priority of distal leg bones is relatively high for caribou (Parker 1989), metatarsus length should be a good index of early nutrition and skeletal growth among adult females. I argue that a female with a short metatarsus length, at a given body weight, has more body reserves available than a female with a longer metatarsus at the same weight, because the long-boned female has a larger overall skeletal size. In contrast, a female with a short mandible might be reproducing for the first time, or may have reproduced at a younger age, i.e., before mandible growth was complete.

The variation in the slope of the relation between pregnancy and body weight or fat between years suggests that caution must be used when estimating pregnancy rate from models 2 or 3, or when combining data across years to create models, since the elevation of the curve describing probability of pregnancy may be sensitive to variation in the body weights of pregnant females between years. Differences in probability of pregnancy

between years may have been caused in part by a confounding effect with annual variation in the proportion of females ceasing and extending lactation; however, "year" was still significant upon exclusion of extended lactation females from logistic regression analyses ($P<0.05$), suggesting that annual variation in some other factor(s) also attributed to its entrance into models 2 and 3.

Limitations of body weight and fat as predictors of pregnancy

Body weight in November was a reasonable predictor of pregnancy for caribou. However, a 10 kg difference of mean body weight among years was not reflected by a change of pregnancy rate, and body weight was inadequate to explain the reduced pregnancy rate of lactating females relative to nonlactating caribou, even when differences of skeletal size and year were removed (model 3). In addition, body weight was unable to account for differences of pregnancy status among lactating females. However, body weight in early October was a good correlate of parturition status (Cameron *et al.* 1993). If body weight is a significant correlate of pregnancy because it is an index of body composition, then variation of alimentary fill between seasons (Adamczewski *et al.* 1987a) and lactation classes (Huot 1989) may partly account for the poorer predictive ability of body weight in November. Increased alimentary fill among lactating females (Huot 1989) would bias estimation of ingesta-free body weight, and therefore the weight of its chemical components, overestimating body fat for lactating caribou relative to nonlactating ones. Therefore, pregnancy rate of lactating females would be lower than predicted from body weight alone, resulting in a downward adjustment of pregnancy rate among lactating females in mathematical models, as seen in model 3. In addition, changes of nutritional status or body weight between early October (immediately prior to the breeding season) and mid-November may affect the relation between body weight and pregnancy status (see below).

Although differences of body fatness accounted for more of the variation in probability of pregnancy than any other variable, the relationship between body fat and fertility for caribou was influenced by both lactation class and year. Caribou that were ceasing lactating were less fat than nonlactating females (Table 7), but had similar pregnancy rates. Moreover, differences of body condition were inadequate to explain the reduced fertility of females that were extending lactation: their probability of pregnancy was nearly 50% less than that of females ceasing lactation while at the same mean body fat content, body weight, and mandible length. Pregnancy rate was also insensitive to changes of body fatness among years: a 2 kg increase of mean body fat resulted in only a 2-4% increase of pregnancy rate.

The relations between body condition and fertility for red deer, like those for caribou, were not entirely attributable to differences of body weight, body size or condition. Like caribou, nonlactating red deer were more fertile than lactating females at a particular body weight (Mitchell and Brown 1974), although this difference of fertility was not seen under farmed conditions (Hamilton and Blaxter 1980). In contrast to caribou, red deer that had raised a calf the previous summer were more (rather than less) fertile than those that had not at the same carcass weight, body fatness, and jaw length (Albon *et al.* 1986). Finally, jaw length for red deer (Albon *et al.* 1986) was inversely related to probability of pregnancy, while for caribou mandible length was directly related to fertility. The reason for these differences between species is unknown, but perhaps differences of ecology of these two species are responsible, rather than some regulatory process. For example, red deer are subject to contest competition with conspecifics within a defined home range (Clutton-Brock *et al.* 1987), while caribou of the Porcupine Herd migrate long distances in spring and autumn (Fancy *et al.* 1989) and therefore are influenced less predictably by density. Such differences in selective pressure might lead to differential responses in the relation between indices of skeletal size and pregnancy rate.

Alternatively, age of females may have affected probability of pregnancy (Albon *et al.* 1986), while detection of age-effects may have required finer resolution of animal age that was attained in this study.

Extended lactation may be evidence of conflict between the female and her offspring over timing of weaning (Trivers 1974), resulting in lactational infertility among some females. During weaning, the mother's strategy includes reduced investment in the current offspring, while increasing investment into future offspring. In contrast, the progeny benefits most from continued maternal investment, and offspring may be able to influence their mother's strategy. For red deer, decreased milk production in response to food limitation induced higher nursing frequencies of offspring, causing late estrous or anestrus in their mothers, perhaps because of elevated prolactin levels (Loudon *et al.* 1983). Although milk production for reindeer is extremely low by 100 d post-calving (White and Luick 1984) and nursing bouts for Rangifer are infrequent (Parker *et al.* 1990; Lavigueur and Barrette 1992), milk nutrients nevertheless could influence calf growth and survival (White 1983, 1992). Therefore, I believe that conflict over termination of maternal investment is strong for caribou, and that offspring which succeed in delaying complete nutritional independence might have a large competitive advantage over weaned calves.

Variation among years in the proportion of caribou ceasing versus extending lactation (from 79.6% ceasing lactation in 1990 to 31.6% in 1992; $P<0.001$) implies that weaning strategy might vary among years for caribou. Differences in timing of weaning may allow females or their calves to compensate for environmental variation of nutrient availability. Berger (1979) hypothesized that different weaning behaviors for bighorn sheep (*Ovis canadensis*) reflected adaptive strategies to different ecological conditions. Changes of timing of nutrient shortage among herds or years would be expected to alter timing of weaning by changing calf growth rate and behavior and the maternal strategy of

investment. For instance, female Dall's sheep (*Ovis dalli*) responded to annual changes of timing of greenup and peak nutrient availability by altering nursing behavior (Rachlow and Bowyer 1994).

Alternatively, maternal nutrition in autumn might affect probability of pregnancy. Nutrient flushing (a short-term increase of nutrition associated with increased ovulation rates and fertility; see I'Anson *et al.* 1991) could account for differences of fertility among years, lactation classes, or body weight categories. In years when high quality forage is available in autumn, relatively lean females might improve in condition more rapidly than fatter females (Chan-McLeod *et al.* 1994), and conception rates of these lean females could rise more markedly in response. An increase in the plasma levels of branched-chain amino acids has been proposed as a nutritional translator to the ovaries for domestic sheep (Downing *et al.* 1990; Smith 1991) and it has been shown for caribou that mushrooms might also be important (White *et al.* 1993). Changes in timing of plant senescence and snowfall (Eastland 1991), could determine the availability of protein-rich food sources in late-summer or autumn, which should result in nutrient flushing (Smith 1991). Finally, rate of weight or fat gain, or food intake during rut and its associated effects on metabolic rate (Kennedy and Mitra 1963) could also trigger subtle changes of reproductive function and vary among years.

That body fat and body weight are not absolute predictors of pregnancy is not unexpected as they do not directly regulate fertility. No convincing evidence currently exists for a nutritional translator, i.e., a direct metabolic pathway linking body condition to the pulse generator of gonadotropin-releasing hormone (Bronson and Manning 1991). Instead, fertility may be linked to energy balance through indicators such as availability of metabolic fuels (Schneider and Wade 1989), branched-chain amino acids (Downing *et al.* 1990; Smith 1991) or variation of insulin levels (Cameron *et al.* 1985 in Bronson and Manning 1991). While body condition may not be an ultimate cause of differences of

fertility, body condition is determined in part by whole body energy balance. Thus it is a useful correlate to fertility, particularly for population management and ecology (Bronson and Manning 1991).

In conclusion, fertility among female caribou was significantly related to body condition and skeletal dimensions. Heavier, short-legged females or fatter, long-jawed females were more likely to be pregnant than light, long-legged or thin, short-jawed females. Lactation significantly affected fertility in two ways: females that had lactated throughout summer and autumn were less likely to be pregnant than nonlactating females at a particular body weight, and females that extended lactation into early November were unlikely to be pregnant regardless of their body condition or skeletal size, suggesting lactational infertility. In addition, the entrance of year into models predicting fertility suggests that complex interannual patterns in the nutrition and ecology of caribou affect the physiological relations between pregnancy and body condition.

CHAPTER 4: GROWTH OF CARIBOU CALVES IN RELATION TO MATERNAL CONDITION[1]

Abstract: Patterns of first-summer growth were characterized in captive and wild maternally-raised arctic caribou calves. Calf growth was then compared with the oversummer weight gain of the calf's dam. Peak growth rates of captive Porcupine Herd and wild Central Arctic and Porcupine Herd calves were similar. Ecological constraints apparently influenced the timing of autumn growth stasis, and therefore body weight of the calf upon entering winter: growth greatly slowed or stopped at 100 d of age for wild calves, but continued for another month or more in captive calves fed a diet containing moderate levels of protein and energy. Caribou therefore have the genetic potential for extended duration of first-summer growth beyond that observed in wild populations. Among wild calves, autumn body weight was influenced by early growth: birth weight and growth rate from birth to 3 weeks of age accounted for nearly 79% of the variation in autumn body weight. Birth weights of wild Porcupine Herd calves were related, in turn, to maternal weight 3 weeks postpartum, implying that females with low body weights during late gestation gave birth to the lightest calves. Finally, birth weights of wild Porcupine and Central Arctic Herd calves were relatively low in 1992. However, weights of calves entering winter were more sensitive to changes in duration of growth than to differences in early growth or maternal body condition 3 weeks post-calving. Captive adult Porcupine Herd females weighed 15 kg more than wild Porcupine Herd females in June. The larger body reserves of captive females may have permitted additional flexibility in milk production, since autumn body weight of captive calves was unrelated to birth weight or early growth. Among Porcupine Herd caribou, captive lactating females and nonlactating wild females gained weight more rapidly than wild lactating females. No

[1]Gerhart, K.L., White, R.G., Cameron, R.D., Russell, D.E., Griffith, D.B. In Prep. Growth of caribou calves in relation to maternal body condition. Can. J. Zool. **00:** 00-00.

compensatory weight gains were evident among adult female Porcupine Herd caribou: those with low June body weights gained weight no more rapidly than heavier females in the same lactation class, and autumn body weight was highly correlated with June body weight.

Introduction

Arctic caribou are constrained by severe environmental conditions to a brief period of abundant, high quality forage. During this short period of high nutrient availability, reproductive females must replenish body fat and protein depots depleted during winter while meeting the high metabolic demands of lactation (White and Luick 1984). These conflicting nutritive demands are each critical to the reproductive success of the female (Clutton-Brock and Godfray 1991): failure to meet the nutritional needs of the current calf may reduce its survival (Haukioja and Salovaara 1978; Clutton-Brock *et al.* 1985) or reproductive potential (Clutton-Brock and Albon 1985; Langvatn 1994), while failure to replenish maternal body reserves will threaten the female's own subsequent reproduction (Cameron *et al.* 1993; Cameron 1994; Chapter 3) and survival (Albon *et l.* 1983a; Clutton-Brock *et al.* 1983).

Variation in the nutritional state of the mother can have a marked effect on calf growth and survival. Maternal nutrition immediately prior to and during lactation affects milk yield (Louca *et al.* 1974) and the rate of nutrient transfer to the neonate (Jacobsen *et al.* 1981; Loudon *et al.* 1984; White and Luick 1984). However, if a high quality diet is available to the female during early lactation, early growth of the calf may be less affected by female nutrition during pregnancy (Rognmo *et al.* 1983), and low birth-weight calves may demonstrate compensatory gains (Rattray 1977; Mueller and Sadlier 1980).

In mainland caribou herds, summer nutrition is inadequate to allow lactating females to regain fat and protein reserves equal to those of females that did not lactate

during summer (Dauphiné 1976; Huot 1989; Tyler 1990; Allaye-Chan 1991; Chapter 1). Since probability of pregnancy is related to autumn body condition (Cameron *et al.* 1993; Cameron and Ver Hoef 1994; Chapter 3), such lactating females are less fertile than their nonlactating counterparts (Chapter 3). Therefore, to maximize lifetime reproductive success, females are expected to have developed evolutionary tradeoffs which balance the costs and benefits of investment in the current calf and accumulation of maternal body reserves. However, little is known about the timing and extent of changes in nutrient allocation priority between milk production (calf growth) and deposition of maternal body reserves in caribou.

The objectives of this study were (1) to characterize the growth pattern of arctic caribou calves, (2) to compare the patterns of weight gain in free-ranging arctic caribou calves with those of captive calves, (3) to relate calf growth to maternal body condition, and (4) to compare apparent allocation strategies and levels of maternal investment in caribou on 2 planes of nutrition.

Methods:

Study populations

Body growth and changes in body condition of wild caribou from 2 adjacent herds were studied. The Central Arctic Herd (CAH) is a relatively small herd of arctic caribou (estimated at 16,000 animals in 1986; Cameron *et al.* 1991) that resides north of the Arctic circle year round (Cameron and Whitten 1979). Seasonal movements of the CAH are modest with considerable overlap between winter and summer distributions (Cameron and Whitten 1979). In contrast, the Porcupine Caribou Herd (PCH) is large (estimated at 156,800 in 1992; Fancy *et al.* 1994) and migratory (Fancy *et al.* 1989; Russell *et al.* 1993). PCH females calve on the coastal plain of Alaska adjacent to the calving ground of the CAH (Whitten and Cameron 1983), and move south into the Yukon Territory or

Interior Alaska during mid to late summer (Fancy *et al.* 1989; Russell *et al.* 1993). Daily movements of females from the 2 herds are similar, except during spring and fall migrations (Fancy *et al.* 1989).

In addition, a population of reproductively active PCH caribou, which had been captured at birth and bottle raised (Parker 1989), were housed at the Large Animal Research Station, Institute of Arctic Biology. Calf birth weight, sex, and birth date were routinely collected, and body weights of calves and their mothers were recorded periodically during growth. Twenty-two calves born to 7 different females ≥ 3 y of age from 1991 to 1994 are included in this study, as are 7 cow-calf pairs.

Determination of growth in wild caribou

During the first week of June in 1992, 80 newborn calves of the PCH were captured on the Arctic coastal plain of Alaska, in the traditional calving grounds of the PCH (Whitten and Cameron 1983; Russell *et al.* 1993). Groups of parturient females were approached by helicopter. When a young calf was seen, the helicopter landed as close as practical to the cow-calf pair, and 2 people were dropped off to capture the calf by hand. Calves that were wet, were not standing, or whose mothers retained afterbirth were avoided. Personnel handling calves wore clean plastic gloves to minimize scent contamination of calves. Each calf was weighed, sexed, and its metatarsus length (mm) measured (Langvatn 1977). Calves were then outfitted with 134 g radiocollars mounted on brown elastic collars. The collars had previously been exposed to sun and vegetation for > 24 h, and were handled exclusively with gloves to avoid scent contamination. The elastic collar had 3 expansion folds and a break-away seam sown with cotton thread to allow for animal growth. Time elapsed from capture to release of newborn calves averaged 90 s. Forty of these calves were subsequently recaptured as part of this study.

Three to four weeks after the initial capture, a subsample of 29 radiocollared PCH calves were relocated, and calves and their mothers were captured separately using a hand-held netgun shot from a helicopter (Bell 206B). Calves and their mothers were weighed, measured, and scored for body condition, and the lactating females were radiocollared. During the same period, an additional 20 radiocollared females that were maintained as part of a calving area study (Whitten *et al.* 1992) and had been pregnant but had lost the calf prior to 24 June, were captured, weighed, measured, and scored for body condition, as above. These females are subsequently referred to as nonlactating.

In mid July, 12 radiocollared calves were recaptured and weighed. In late September, 14 nonlactating and 7 lactating female caribou were recaptured, as were 12 calves and 4 females that had lost their calves since late June. Caribou were weighed, measured, and scored for body condition, as above. Low clouds prevented the search of mountainous areas for collared caribou in autumn; thus I was unable to account for all missing animals and possible mortalities.

Newborn CAH calves were similarly collected on foot with the aid of a helicopter in early June. However, CAH neonates were killed with a captive bolt-gun, and analyzed for chemical composition (Chapter 1). Older CAH calves were collected at random from a helicopter with a 22 rifle at 4, 6, and 19 weeks after peak calving, again to determine chemical composition. In addition, four 3-week old PCH calves that were injured or orphaned during capture operations, and five 17-week old PCH calves were sacrificed for comparison of chemical composition between herds.

Comparisons between herds

Growth rates of CAH calves were determined from the difference between mean body weights at each collection, calculated assuming a birth date of 5 June (the approximate peak of calving). For the PCH, consecutive body weights of individual wild

and captive calves were used to estimate growth rate, except as noted. Differences in growth between sexes and herds were tested using analysis of variance for unbalanced data (GLM in SAS).

Body fat content of adult caribou was estimated using a relation between fatness and the product of body condition score and body weight, which was previously validated for caribou (Gerhart *et al.* 1992; Chapter 2):

$$Log_e(\text{Body fat, kg}) = -7.713 + 1.444\ Log_e(\text{BCS*BW}),\ r = 0.928,\ SE = 0.33.$$

Results:

Growth of free-ranging caribou calves

Growth patterns of wild caribou calves were similar when examined using either longitudinal (PCH) or cross-sectional data (CAH) (Table 10). No differences in body weight or body composition (Chapter 1) were detected between wild CAH and PCH calves at birth, 3-4, 6 or 15-19 weeks. Wild calves of both the CAH and PCH showed a rapid increase in body weight from birth to 21-28 d (for the PCH, 373 ± 9 g/d, range 346 to 483; for the CAH, 402 g/d) followed by a period of slower growth from 28-44 d (for the PCH 335 ± 18 g/d; for the CAH, 306 g/d;). Growth was undetectable ($P = 0.5$) from 100 to 134 d (Figure 14); therefore, when estimating growth rates from 6 weeks to autumn (405 g/d for the PCH, and 374 g/d for the CAH), I assumed that growth ceased at 100 d. Uncorrected rate of gain from 3 to 17 weeks of age for the PCH was 251 ± 21 g/d.

Differences between sexes increased with age. At birth, no difference between sexes was discernible for body weight, metatarsus length or body condition score of wild PCH or CAH calves. By 3 weeks of age, male PCH calves weighed 1.6 kg more than female calves ($P = 0.031$), and had longer mandible ($P = 0.055$) but not metatarsus ($P = 0.13$) lengths. Average weight gain (kg) from birth to 3 weeks of male PCH calves was greater than that of females ($P = 0.033$), although rates of gain (g/d) did not differ

Table 10. Weights of caribou during first-summer growth. Mean body weights ± SE (and sample size) at birth and throughout first summer growth in free-ranging caribou of the Central Arctic (CAH) and Porcupine Herds (PCH), and in captive Porcupine Herd caribou.

Herd	0 days (n)	21-28 days (n)	40-44 days (n)	100-105 days (n)	115-130 days (n)
Free-ranging population					
CAH	5.65 ± 0.21^{a} (10)	16.91 ± 1.06^{a} (6)	22.09 ± 1.16^{a} (10)	NA	44.97 ± 2.38^{a} (10)
PCH[1]	$6.44 \pm 0.13^{a,b}$ (40)	15.15 ± 0.35^{a} (29)	22.10 ± 0.56^{a} (12)	43.79 ± 2.10^{a} (5)	42.53 ± 1.49^{a} (12)
Captive population					
PCH[1]	6.96 ± 0.23^{b} (22)	16.08 ± 0.71^{a} (11)	22.17 ± 0.68^{a} (16)	46.50 ± 1.40^{a} (10)	55.70 ± 1.94^{b} (17)

[1]Repeated measurements on subsets of the same group of individuals across time, except for wild calves killed at 100-105 d.

Note: Means with different letters within a column are significantly different ($P<0.05$).

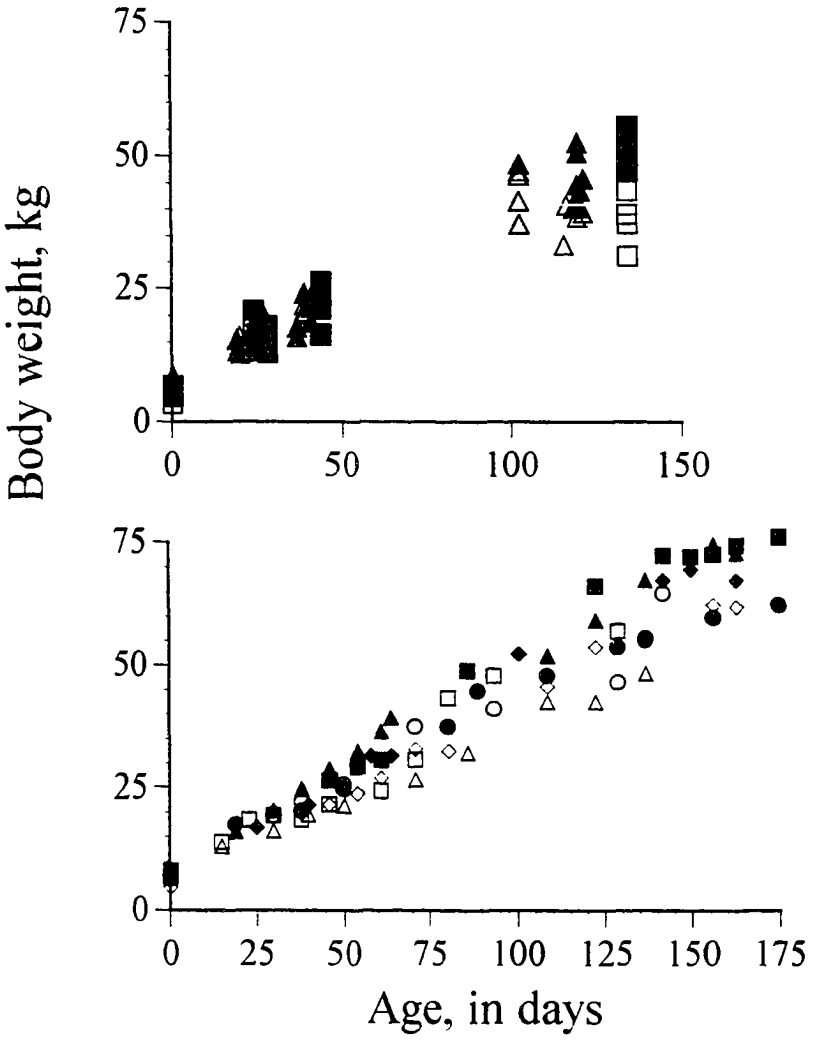

Figure 14. Growth patterns of wild and captive arctic caribou. Body weight in relation to age for wild Central Arctic (squares) and Porcupine Herd (triangles) caribou (upper figure), and individual captive Porcupine Herd caribou (lower figure) during first summer growth. Solid symbols represent males, and open symbols females.

discernibly ($P = 0.29$). Three week old female PCH calves had higher body condition scores than did male calves ($P = 0.039$), in agreement with chemical analyses of CAH calves showing that females are fatter than males at this age (Chapter 1). However, by six weeks of age differences of body weight and fatness between male and female calves were not discernible ($P = 0.61$ and 0.24, respectively). In autumn, 17 week old male PCH calves weighed 7.5 kg more than female calves ($P = 0.013$), a difference between sexes similar to that of calves which were sacrificed for determination of chemical composition (10.8 and 6.5 kg for 19 week old CAH and 15 week old PCH calves, respectively). Males had longer metatarsus bones than females in autumn ($P = 0.015$), but mandible lengths ($P = 0.29$) did not differ between sexes. Males had larger absolute gains in body weight from birth to 17 weeks (38.9 versus 30.9 kg, $P = 0.028$), and had higher rates of gain from birth (326 versus 264 g/d, $P = 0.04$) than did female calves; however, rates of gain from 3-17 weeks did not differ between sexes ($P = 0.43$). While no individual calf was weighed at both 15 and 19 weeks of age, the data suggest that male calves may have continued to gain weight at a greatly reduced rate (97 g/d) during this period, since mean body weight of male calves increased between 100 and 135 d (Fig. 14).

Early growth of a calf was a good predictor of its body weight throughout summer. Body weights of individual PCH calves at 3 weeks post partum were strongly related to both birth weight and growth rate from 0 to 3 weeks ($P = 0.007$ and 0.0001, respectively). Birth weight and sex explained 63% of the variance in autumn weight, while birth weight and growth rate from 0 to 3 weeks explained 78.6% of the variance in body weight at 17 weeks. In addition, calf body condition score at 3 weeks explained 61% of the variance in calf body weight at 6 weeks ($P = 0.012$).

Rate of early growth also may have influenced calf survival. Calves recaptured in autumn had demonstrated higher than average rates of early growth (399 g/d). When captured at 3 weeks, calves recaptured at 17 weeks had been heavier than the average calf

(by 0.5 kg for males, and 0.7 kg for females) but these calves had not been heavier than average at birth.

Growth in captive caribou

Growth patterns of captive caribou were similar to those of their wild counterparts. At 3-4, 6, and 15 weeks post-calving, no significant differences were found between mean body weights of captive and wild populations. Growth rates from birth to 3 weeks (415 ± 27 g/d, range 217 to 548) were more variable among captive than wild caribou, as were birth weights (CV = 0.76 vs. 0.26%, for captive and wild PCH caribou, respectively). Mean birth weight of captive PCH calves was 1.3 kg heavier than that of wild CAH calves ($P < 0.05$). However, birth weights of captive PCH calves were not significantly greater than those of wild-born PCH calves in 1992. Birth weights did not differ between sexes ($P = 0.11$). Captive male calves were not heavier than females at 3 weeks of age ($P = 0.10$), but were 5.2 kg heavier at 6 weeks ($P = 0.002$). By 135 d of age, males were 9.3 kg heavier than females ($P = 0.031$). Growth rates from 0 to 19 weeks of age varied with sex, and averaged 382 ± 18 g/d for males and 325 ± 19 g/d for females ($P = 0.04$).

Duration of first-summer growth varied between wild and captive populations. Unlike wild caribou, captive calves continued to grow past 100 d (15 weeks) of age. Among captive calves, growth rate from 15 to 19 weeks of age (308 ± 38 g/d) was not markedly slower than earlier growth. Captive caribou therefore were significantly heavier than wild calves by 135 d of age (Table 10). Maximum autumn weight of captive calves, attained between 124 and 226 days post-calving, was 18 kg heavier than that of wild calves. Timing of onset of growth stasis varied independently of sex. Maximum autumn weight was not correlated to birth weight ($P = 0.35$).

Body condition of lactating and nonlactating females

Body fat content of wild nonlactating PCH females in late June was 0.9 kg greater than that of wild lactating females ($P = 0.001$), although body weights of lactating and nonlactating females did not differ significantly ($P = 0.069$) (Table 11). In autumn, wild nonlactating females were 7.3 kg heavier than lactating females ($P = 0.018$), and had 2.9 kg more fat ($P = 0.0003$). Nonlactating females demonstrated the highest rates of weight gain, while females that had lost their calves between late June and September had the lowest gain rate, and gains of lactating females with surviving calves were intermediate.

Captive lactating PCH caribou were heavier than their wild counterparts (by 14.3 and 20.5 kg at 3 weeks post partum and in autumn, respectively), and were also heavier than nonlactating wild females (by 10.5 and 13.3 kg in June and October, respectively; $P < 0.005$ in all cases). Nonlactating captive caribou had body weights similar to those of captive lactating caribou, but small sample size precluded statistical analyses.

Maternal body weight at 3 weeks post partum was highly correlated to autumn body weight for all adult female caribou, regardless of lactation status or captivity (Fig. 15, $r = 0.90$, $P \leq 0.0003$). Amounts of weight gained oversummer were not markedly different among wild lactating, wild nonlactating, and captive lactating caribou ($P = 0.083$, average gain 14.2 kg), despite large differences in both apparent nutritional status and body weight 3 weeks post-partum. Amounts of weight gained between peak lactation (late June) and autumn was not correlated to late June weight for lactating or nonlactating wild PCH females ($P = 0.43$ and 0.73, respectively) but the relation was marginally significant for captive lactating females ($P = 0.075$).

Weight gains of cow-calf pairs

Among wild PCH caribou, maternal body weight in late June was significantly related to calf birth weight ($P = 0.033$). Maternal weight was marginally related to calf

Table 11. Mean body weights and rates of gain ± SE (and sample size) of adult female caribou of the Porcupine Herd during lactation.

	Body weight (kg) 3 wk. post-partum	Body fat (kg) 3 wk. post-partum	Body weight (kg) in autumn	Body fat (kg) in autumn	Rate of gain g/d
Free-ranging PCH					
Lactating	78.5 ± 1.5^{a} (25)	2.16 ± 0.14^{a} (29)	90.0 ± 3.1^{a} (8)	3.83 ± 0.51^{a} (8)	132.1 ± 13.1^{a}
Calf-loss	80.3 ± 1.1^{a} (4)	$2.62 \pm 0.40^{a,b}$ (4)	89.1 ± 1.6^{a} (4)	4.36 ± 0.73^{a} (4)	98.6 ± 9.6^{b}
Nonlactating	82.6 ± 1.6^{a} (20)	3.09 ± 0.18^{b} (19)	97.0 ± 1.7^{b} (13)	6.95 ± 0.42^{b} (12)	159.5 ± 6.7^{c}
Captive PCH					
Lactating	93.1 ± 2.9^{b} (7)	NA	110.3 ± 2.6^{c} (7)	NA	171.7 ± 8.8^{c}

Note: Means within a column with different letters are significantly different ($P < 0.05$)

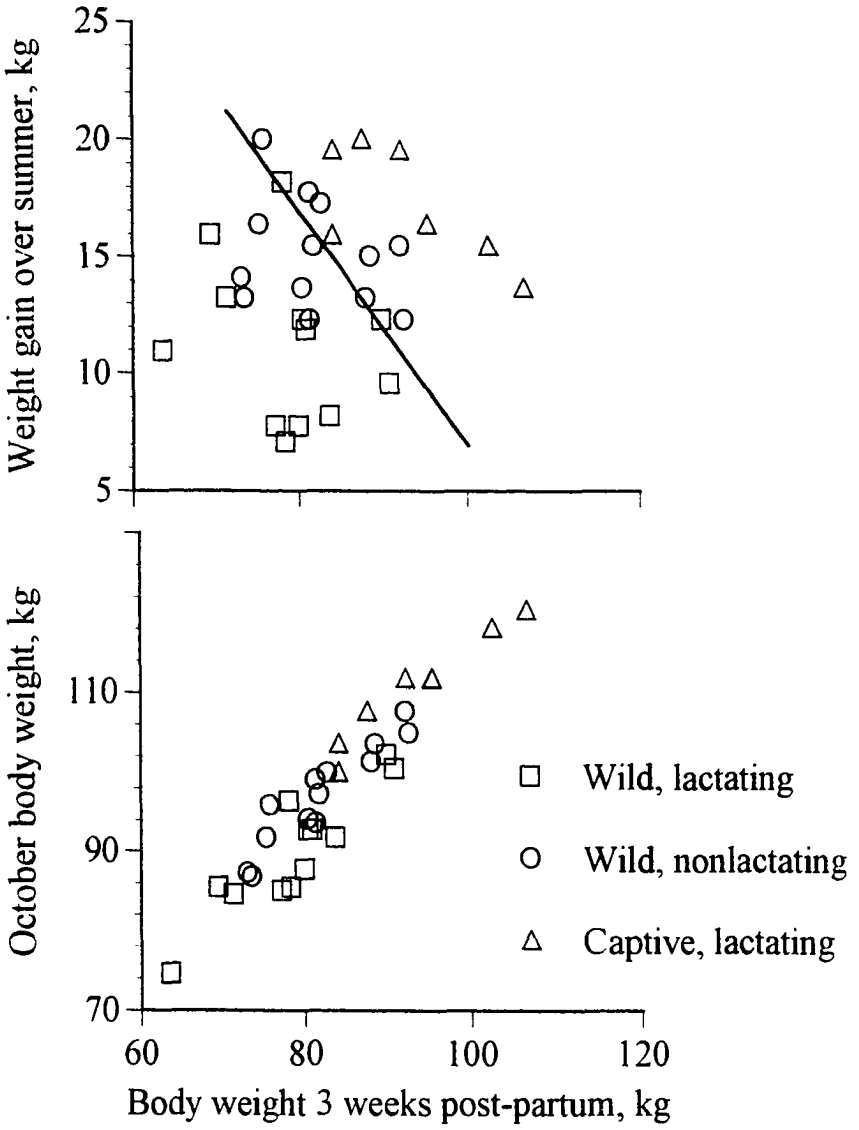

Figure 15. Lack of evidence for compensatory growth among adult female Porcupine Herd caribou. Line in upper figure represents expected relation if a seasonal target weight existed (i.e., demonstration of compensatory growth). Lower figure shows the presence of a strong relation between June body weight and autumn body weight (r = 0.90).

body weight at 3 weeks post-partum ($P = 0.074$), but this relationship was not significant once differences in birth weight were accounted for ($P = 0.48$). Calf weight gain (kg) and rate of gain (g/d) from birth to 3 weeks of age were not related to maternal body weight, and maternal body condition score in late June was not related to calf growth. Weight of calf and dam were not related in autumn; however, sample size was extremely small (n = 5).

For captive caribou, maternal body weight one week prior to calving was related to calf birth weight ($P = 0.036$), and was marginally related to maternal body weight 3 weeks post-partum ($P = 0.07$). However, maternal body weight 3 weeks postpartum was not related to calf birth weight ($P = 0.27$), but was related to calf weight at 3 weeks of age ($P = 0.041$). Weights of calves and their mothers were weakly related in autumn ($P = 0.088$).

Discussion:

Early calf growth rate in cervids is highly correlated with milk intake (White and Luick 1984; Loudon and Milne 1985) and the protein content of that milk (White and Luick 1984; Tyler 1987a), while milk production, and especially protein and lactose content (Chan-McLeod *et al.* 1994), are correlated with forage biomass and quality (Loudon and Milne 1985). Thus high calf growth rates suggest high milk production, which in turn connotes high quality, readily available forage. For caribou, however, maternal body reserves also may influence milk production, regardless of forage quality. Female caribou mobilize body reserves to meet the costs of early lactation (White and Luick 1984), especially during years when calves are born before complete snowmelt

(Eastland 1991). Most mobilization of body reserves occurs in the first 3 weeks post-calving (Tyler 1987a), after which females are exceptionally lean (Dauphiné 1976; Adamczewski *et al.* 1987a; Tyler 1987a; Allaye-Chan 1991; Chapter 1). In agreement, body fat reserves of lactating PCH caribou in late June were 0.9 kg lower than those of nonlactating females that had also born the costs of gestation. Thus, milk production and calf growth during early lactation are determined by both maternal body reserves and nutrient availability during early lactation in caribou.

Among older calves too, milk may be critical to maintaining or enhancing growth. Caribou calves become increasingly nutritionally independent after approximately 40 d of age, as indicated by milk intake (White and Luick 1984; Parker *et al.* 1990), suckling rate (Parker *et al.* 1990; Lavigueur and Barrette 1992), and forage content of the rumen (Gerhart, unpublished data). However, milk protein and energy are more efficiently assimilated than rumen metabolites (White 1992). Therefore, calves may meet maintenance requirements from rumen metabolites, while preferentially allocating nutrients from milk to growth (White 1992).

Patterns of calf growth

Nutrition of the PCH during the winter of 1991-92 may have been inadequate to support both maternal maintenance and maximal fetal growth. June calf survival in the PCH was the lowest on record in 1992 (57%) (Fancy *et al.* 1994), and calf mortality during the winter of 1991-92 had also been exceptionally high (Fancy *et al.* 1994). Both poor neonatal survival (Rognmo *et al.* 1983; Skogland 1985; Cameron *et al.* 1993) and low over-winter survival of juveniles (see Fowler 1987) indicate winter undernutrition. Moreover, birth weights of wild PCH calves that survived to 3 weeks of age in 1992 were lower than those of PCH calves caught at random in other years (Whitten *et al.* 1992),

although they were similar to birth weights of CAH calves in the same year. Low calf birth weights too are associated with maternal undernutrition during winter (Thorne *et al.* 1976; Verme 1977; Blaxter and Hamilton 1980; Espmark 1980; Rognmo *et al.* 1983; Bartmann 1986).

Winter undernutrition may be a relatively common cause of neonatal mortality among arctic caribou: early calf mortality has been associated with low maternal body weight in the CAH (Cameron *et al.* 1993), while most calf mortality in the PCH (59-74%) occurs within the first 48 hours after birth (Whitten *et al.* 1992) and is caused by stillbirth, emaciation, or malnourishment (Roffe 1993). Whether winter undernutrition of arctic caribou is generally caused by stochastic weather events (Russell *et al.* 1995) or is evidence of density-dependent resource limitation (Cameron 1995) remains unclear.

The growth rates of both CAH and PCH caribou between birth and 3-4 weeks of age appear to be near the genetically-determined maximum for the species. Growth rates of captive PCH calves (415 g/d) and of wild calves (373 g/d in the PCH; 403 in the CAH) are similar to those reported for captive maternally-raised caribou of the George River (365-488 g/d; Crête *et al.* 1993) and Delta herds (428 g/d; Parker *et al.* 1990), as well as for wild calves from the Leaf River Herd (377 g/d; Crête and Huot 1993).

Even though early growth rates were relatively high, PCH calves were unable to compensate for early undernutrition during their first-summer of growth. Birth weight and growth rate from birth to 3-4 weeks of age accounted for 78.6% of the variation in autumn body weight of wild PCH calves, although individual birth weights were not correlated with early rates of gain ($P = 0.11$). Thus, calves with low birth weights and calves that grew relatively slowly in early summer had lower body weights in autumn. In addition, birth weights of wild calves were related to maternal weight 3 weeks postpartum, suggesting that females with low body weights during late gestation gave birth to the smallest calves. Finally, calves with low growth rates may have been more

vulnerable to mortality: calves recaptured in autumn had above average growth rates from 0 to 3-4 weeks of age. Similarly, light or late-born red deer are substantially more likely to die during their first summer (Guinness *et al.* 1978b) or winter (Clutton-Brock and Albon 1990); in red deer, this effect increases with density (Clutton-Brock and Albon 1990).

Lactating CAH and PCH caribou are apparently unable to produce enough milk to maintain the growth of their calves during periods of energetic stress. For instance, I reported decreases in fatness (Chapter 1) and growth rate of caribou calves from 4 to 6 weeks of age, a period typified by variable levels of insect harassment (Dau 1986; Russell *et al.* 1993). During insect harassment, activity increases at the expense of time spent foraging and resting (White *et al.* 1975; Reimers 1980); therefore, energy balance becomes increasingly negative. This negative energy balance is expected to reduce milk production, since lactating females can support only minimal milk production from body reserves by late June (Table 11 and Chapter 1). Therefore, periods of energetic stress, such as those caused by insect harassment, are expected to reduce calf growth rates.

The nutritional shortfall resulting from insect harassment may cause calves to switch from maximizing growth (the high milk-ingestion strategy), to an increased reliance on forage, and a corresponding lowering of growth potential, as reported for red deer (Loudon and Kay 1984; Kay 1985). In addition, during and immediately after the insect harassment season, calves of poor-condition females may have increased risk of mortality (Helle and Kojola 1994), as demonstrated by the disappearance of PCH calves whose mothers had low rates of oversummer weight gain (Table 11). An alternative explanation for loss of calves in mid summer may be that lactating females with inadequate rates of maternal weight gain wean their offspring at an earlier age than other females, in an attempt to maintain maternal weight gain and therefore increase likelihood of maternal survival overwinter. Calves of such females would then be forced to subsist purely on

forage, and might be more susceptible to various mortality factors: late weaning is correlated with increased survival overwinter (Clutton-Brock and Albon 1990). However, caribou calves can survive winter without their mothers (Russell *et al.* 1991). In either case, a low rate of growth and a decline in body reserves mid-summer might provide a lethal set-back to a low-birth weight calf.

Calf growth rate throughout the first summer is critical to survival: reductions in autumn body weight of calves are correlated with reduced overwinter survival (Clutton-Brock *et al.* 1987; Helle *et al.* 1987; Cederlund *et al.* 1991). In addition, in reindeer, body weight at approximately 2 months of age is significantly correlated with chances of survival during the first year of life (Haukioja and Salovaara 1978). During the period of insect harassment and reduced growth (4 to 6 weeks of age), growth rates of wild CAH and PCH caribou were similar to those of George River Herd calves (268 g/d; Crête and Huot 1993), which are thought to be affected by poor summer range quality (Messier *et al.* 1988; Couterier *et al.* 1990; Crête *et al.* 1993; Crête and Huot 1993).

The dramatic reduction in both weight gain and skeletal growth of wild calves after approximately 100 d of age may indicate protein limitation (Jagusch *et al.* 1970), or a change in nutrient allocation from lean body growth to adipose deposition (Verme and Ozoga 1980b), perhaps initiated by shortening day length (Abbot *et al.* 1984). The absence of an early growth plateau in captive calves suggests that timing of growth stasis is determined in part by nutrition. Similar growth plateaus have been documented in other free-ranging *Rangifer* populations: body weight of semi-domestic reindeer calves increases only 5% between September and January (Petersson and Danell 1993), while skeletal growth of wild reindeer declines 50-60 d after birth (Skogland 1983). In addition, body growth plateaued at 4-4.5 months in wild caribou (McEwan 1968), while captive caribou continued to increase in weight until May (McEwan 1968). Captive caribou from

the George River Herd also grew until between 120 and 140 d of age (Crête *et al.* 1993), although growth rates slowed after 80 to 100 d of age (Lavigueur and Barrette 1992).

Sex differences

I suggest that differences in birth weight between sexes may be reduced by inadequate winter nutrition. Birth weights of male reindeer and caribou calves are widely reported to be greater than those of female calves (Lavigueur and Barrette 1992; Kojola 1993; Adams *et al.* 1995), as are autumn body weights (McEwan 1968; Dauphiné 1976; Lavigueur and Barrette 1992; Petersson and Danell 1993). Lavigueur and Barrette (1992) found that sex differences in body weight at birth were maintained until autumn among captive George River Herd caribou. In contrast, wild male calves of the CAH and PCH were 7.4% larger than females at birth, and 17.7% larger in autumn. In addition, differences in birth weight between sexes were not significant for wild CAH or PCH caribou in 1992, although birth weights of wild male PCH calves in 1983-1985 had been greater than those of females (Whitten *et al.* 1992). Faster growth rates of males after birth may be caused by differences in the efficiency with which available energy is converted into body mass, perhaps associated with sexual differences in hormonal activity (Boyd and McCann 1989), or different patterns of resource allocation between activity and growth (Byers and Moodie 1990). Alternatively, mothers may invest more resources into male offspring both prior to birth and during growth (Trivers and Willard 1973).

Compensatory growth

There was no evidence of compensatory gains during summer for adult female PCH caribou, in contrast to weight gain patterns in mule deer (Renecker and Samuel 1991), wapiti (Hudson *et al.* 1985), and nonlactating CAH caribou (Cameron and White 1995). Body weight gains between peak lactation (late June) and autumn were not related

to minimum body weights (late June); instead, June and autumn body weights were strongly related (r = 0.9). Regardless of reproductive status or captivity, PCH females gained approximately 14 kg during summer. These results may imply that nutrition, especially energy intake (Chan-McLeod *et al.* 1994), limited weight gains to below the target weight for all caribou, or that environmental variability or changes in population density have obscured selection for target weights in this population

Maternal investment

In spite of greater maternal body weights, birth weights of captive PCH calves were not significantly larger than those of their wild counterparts, suggesting that captive PCH females invested proportionately less into fetal growth. In addition, rates of growth for captive and wild PCH caribou did not differ significantly, although captive maternal females were 15 kg heavier and had greater protein availability over winter. While birth weights may be genetically constrained, it is unlikely that calf birth weight in 1992 was at the genetic maximum, since birth weights of wild PCH calves were up to 1.7 kg heavier a decade ago (Whitten *et al.* 1992). Instead, the 3 to 5 y old captive females may have been too young to have reached peak productivity (e.g., Guinness *et al.* 1978a; Lenvik *et al.* 1988).

Captive lactating caribou did not mobilize maternal reserves during lactation to the extent that wild females did. While energy limitation experienced by wild caribou may be responsible for their leanness, captive females may have had adequate energy available to maximize both milk production and deposition of maternal reserves (Chan-McLeod *et al.* 1994). For instance, calves of captive caribou were apparently able to compensate for low rates of early growth. Among captive calves, neither birth weight nor early growth rate was significantly related to autumn calf weight, whether it was measured at 100, 135, or >135 d of age. While the additional variability in growth rates of captive calves and the

small sample size may have precluded detection of correlations, the larger body reserves of captive females (Table 11) also may have permitted mothers of small calves to produce additional milk, enabling small captive calves to maximize both rate and duration of growth, and leading to compensation prior to winter. Finally, weak or malnourished calves that would have died shortly after birth in the wild may have survived in captivity, since captive calves are protected from predation and insect harassment, have reduced daily costs of activity, and have ad libitum access to high quality forage.

In conclusion, poor nutrition overwinter appeared to affect calf birth weight and growth of PCH calves in June of 1992. Birth weights of wild PCH calves were related to maternal weight 3 weeks postpartum, implying that females with low body weights gave birth to the smallest calves. Summer nutrition was not adequate to allow compensatory growth of PCH calves: differences in birth weight and early growth rate accounted for nearly 79% of the variation in autumn body weight. Increased energy expenditure and decreased feeding time caused by insect harassment may have resulted in the observed reduction in growth rates and fat content of wild calves in July. Nutrient availability also may have influenced the onset of growth stasis: growth greatly slowed or stopped at 100 d of age for wild PCH and CAH calves, but continued for another month or more in captive PCH calves offered a moderate protein and energy diet. Captive females and nonlactating females gained weight more rapidly than wild lactating females. No compensatory weight gains during summer were evident: autumn body weight of adult females was highly correlated with June body weight. Calf weight entering winter was more sensitive to changes in the duration of growth than to differences in peak growth rate or maternal body condition during peak lactation.

SYNOPSIS

It has been speculated that large, migratory populations of caribou were limited by predation and/or hunting (Bergerud 1980), however, it does not now appear that these populations are limited by predators (Messier *et al.* 1988); therefore, population regulation is expected to occur by density-dependent mechanisms, most likely via nutrition. While demonstration of density-dependent regulation requires long term data, physiological responses of large mammals to density-independent and density-dependent nutrient limitation are likely similar (Caughley and Krebs 1983). Therefore, the mechanisms linking nutrient limitation and herd productivity can be investigated using short-term data.

Calf production and survival are major determinants of herd productivity (Fancy *et al.* 1994). Reproductive output of a female may be influenced by both intrinsic and extrinsic factors (Bailey 1991). Intrinsic factors include age (Guinness *et al.* 1978a; Albon *et al.* 1986) and previous reproductive effort (Guinness *et al.* 1978a; Cameron 1994; Cameron and Ver Hoef 1994), as well as individual characteristics such as genetic makeup (Pemberton *et al.* 1991) and social status (Kojola 1989; Clutton-Brock and Albon 1990). Intrinsic factors also incorporate those related to year of birth, which affect individual growth, development, and survival (Albon *et al.* 1987; Langvatn 1994). Extrinsic factors comprise the ecological density of the population (density-dependent factors) (e.g., Albon *et al.* 1983a; Festa-Bianchet 1988) and stochastic environmental effects (density-independent factors) such as winter snow depths and summer foraging conditions (e.g., Albon *et al.* 1983b; Clutton-Brock and Albon 1990; Russell *et al* 1993). The interaction of these factors largely determines potential reproductive output (Bailey 1991).

I hypothesize that there are points in time ('decision' points) during which these intrinsic and extrinsic factors interact with nutrient availability to determine how female caribou allocate their resources between maternal needs and calf growth. My research focused primarily on the effects of previous reproductive effort and nutrition on body reserves, calf growth, and pregnancy rate of female arctic caribou.

Gestation and calving success

Although I did not directly investigate the influence of winter nutrition of *Rangifer* on reproductive success, a credible scenario can be extracted from the literature. In late winter, a pregnant female with reserves that are inadequate to support fetal growth and maternal maintenance will reduce allocation to the fetus, producing a small neonate (Thorne *et al.* 1976; Rattray 1977; Verme 1977; Blaxter and Hamilton 1979; Espmark 1980; Rognmo *et al.* 1983; Skogland 1984); hence, the correlation between low maternal body weights in late winter and low neonatal weights (Varo and Varo 1971; Bergerud 1975; Haukoija and Salovaara 1978; Rognmo *et al.* 1983; Skogland 1983, 1984; Clutton-Brock and Albon 1990). Also, that female is likely to calve late (Cameron *et al.* 1993), perhaps extending gestation in an attempt to increase calf birth weight (Berger 1992). The consequences are severe either way. Both low birth weight (Rattray 1977; Guinness *et al.* 1978b; Clutton-Brock and Albon 1990; Whitten *et al.* 1992) and late-born (Guinness *et al.* 1978b; Festa-Bianchet 1988; Clutton-Brock and Albon 1990; Adams *et al.* 1995) calves have higher mortality rates than other calves. In addition, malnourished mothers are less attentive (Lent 1974), thus their calves are more vulnerable to predation, abandonment, or injury. The end result of maternal undernutrition in late winter is a reduction in calf survival.

For arctic caribou, the amount of maternal body protein accrued prior to conception may be as important to fetal growth as maternal nutrition during gestation. The winter diet of PCH caribou is comprised primarily of lichens (Russell *et al.* 1993), and that of the CAH is assumed to be roughly similar, although lichens are less available (White *et al.* 1975). Lichens have a very low protein and mineral content (Jacobsen and Skjenneberg 1976); thus, caribou are unlikely to deposit body protein during winter. Instead, as shown in Chapter 1, they catabolize a significant proportion of their existing protein reserves (see also Adamczewski *et al.* 1987a; Huot 1989). However, PCH

females with larger protein reserves during late pregnancy grow larger fetuses (Allaye-Chan 1991), and those CAH caribou with low body weights shortly after parturition produce calves that are more likely to die at or shortly after birth (Cameron *et al.* 1993). Thus, the amount of body protein accumulated during the previous growing season is expected to influence calf birth weight and survival in caribou, as does nutrition during gestation.

Lactation and calf growth

After parturition, calf growth and maternal nutrition are linked via milk production. Adequate maternal protein and energy reserves are critical to early milk production, since greenup may occur up to two weeks after parturition (Eastland 1991; Russell *et al.* 1993). Lactating females mobilize body fat (Cameron and Luick 1972; Vernon and Flint 1984; Tyler 1987a), which supports synthesis of lactose and other milk constituents (Luick *et al.* 1983; Chan-McLeod *et al.* 1994). Irrespective of timing of greenup, however, body reserves of maternal females are mobilized during early lactation, as evidenced by their extremely poor condition approximately 3 weeks post-calving (Dauphiné 1976; Parker *et al.* 1990; Allaye-Chan 1991; Chapter 1), about or immediately following the peak of lactation (White and Luick 1984; Parker *et al.* 1990). Calf growth, in turn, is directly related to milk yield throughout early lactation (Loudon *et al.* 1983a; White and Luick 1984; Loudon and Milne 1985; White 1992), as well as to the protein content of that milk (White and Luick 1984).

Lactating caribou and their calves are vulnerable to energy or protein shortages when maternal body reserves are low. If summer nutrition is inadequate to support both maternal maintenance and milk production, the female is expected to allocate nutrients first to maternal maintenance, including essential protein requirements, then to milk production (Chan-McLeod *et al.* 1994). Thus, females that are unable to meet maternal

maintenance requirements produce little or no milk, and the calves of those females are forced to rely more on forage. For instance, calves of poorly nourished red deer females that produce little milk are nutritionally independent sooner than those of well-nourished females with high yields of milk (Loudon *et al.* 1983a; Loudon and Kay 1984; Kay 1985). Kay (1985) hypothesized that calves of low-yield mothers graze from an earlier age as a result of hunger, and the low amino-acid:energy ratio of rumen fermentation products lowers growth rate. Alternatively, forage ingested by nursing calves may be allocated primarily to maintenance, while nutrients from milk are preferentially allocated to growth (White 1992). Growth rates of older, ruminating caribou calves (> 3 weeks of age) are highly correlated with milk intake (White 1992).

Lactating CAH and PCH caribou are apparently unable to produce enough milk to maintain the growth of their calves during periods of energetic stress. For instance, I reported decreases in fatness (Chapter 1) and growth rate (Chapter 4) of caribou calves during insect harassment. Clearly, by late June these lactating females can support only minimal milk production from body reserves (Chapter 1). The nutritional shortfall resulting from insect harassment may cause calves to switch from maximizing growth (the high milk-ingestion strategy) to more reliance on forage and a correspondingly lower growth potential, as reported for red deer (Loudon and Kay 1984; Kay 1985). In addition, during and immediately after the insect harassment season, calves of poor-condition females may have increased risk of mortality, as demonstrated by the disappearance of PCH calves whose mothers had low rates of oversummer weight gain (Chapter 4).

An alternative explanation for loss of calves in midsummer may be that lactating females of low body weight gain wean their offspring at an earlier age than other females in an attempt to maintain their weight gain, thereby increasing their likelihood of overwinter survival. Calves of such females would then be forced to subsist purely on

forage and might be more susceptible to various mortality factors: late weaning is correlated with increased survival overwinter (Clutton-Brock and Albon 1990). In either case, a low rate of growth and a decline in body reserves mid-summer might prove lethal to a low-birth weight calf.

Under conditions where nutrition is adequate to meet maternal requirements for maintenance, milk production is expected to reflect nutrient availability (Loudon *et al.* 1983b; Loudon and Milne 1985). In agreement, milk production of reindeer is relatively plastic (White and Luick 1984). Milk production in caribou supported high rates of early growth which did not vary appreciably within the range of nutrition included in this study. Rates of growth from 0 to 3 weeks of age and from 6 to 15 weeks of age were similar between free-ranging CAH and PCH calves and captive PCH calves (Chapter 4). This is presumptive evidence that peak growth rates of wild calves were near their genetically determined maximum, provided that growth of captive calves was not depressed by some unknown dietary insufficiency. However, growth rates of maternally-raised calves at separate facilities are similar to those of LARS calves (McEwan 1968; Crête *et al.* 1993), suggesting that the LARS diet is of high quality. Thus, the hypothesis that wild calves can nearly maximize growth for part of the summer is supported by these data.

In contrast to rate of growth, duration of first-summer growth varied between wild and captive populations. Growth of wild calves declined greatly or stopped by 100 d, as reported in another wild *Rangifer* population (McEwan 1968). Autumn growth cessation has been associated with plant senescence in the Arctic (White *et al.* 1975). However, captive caribou continued linear growth into early winter (approximately 175 d of age; Chapter 4) when they were provided with a ration with moderate to high levels of protein, minerals, and energy. Similarly, other researchers have documented growth to 170 d in captive calves (McEwan 1968; Parker 1989). Parker (1989) suggested that there is a physiological time limit to first-year weight gain in caribou; I suggest that if such a

physiological limit exists, it is determined in part by plane of nutrition, and therefore may be influenced by timing of weaning or plant senescence.

Adult compensatory gain

Data from adult PCH females did not support the hypothesis that summer body weight changes are regulated or adjusted to achieve some target body weight in autumn (sensu Renecker and Samuel 1991). Weight gains of PCH females during summer (June - October; Chapter 4) were no greater among caribou with low June body weights than among those with high body weights in June. All PCH females, whether captive or wild, lactating or nonlactating, gained approximately 14 kg between late June (peak lactation) and autumn (Fig. 15). In contrast, Cameron and White (1995) showed compensatory gains among nonlactating CAH females. I conclude that either the data for CAH females is confounded by reproductive status (pregnancy status of nonlactating CAH females during the previous winter was unknown) or that weight gains in the PCH and CAH are controlled by separate regulatory factors. For instance, Cameron (1995) suggested that the CAH exhibits evidence of density-dependent control on fecundity, whereas Russell *et al.* (1995) showed that stochastic environmental events explain 96% of the changes in fecundity for the PCH over the last decade.

In spite of differences in summer weight gains of CAH and PCH females, autumn body weights and fatness of females from both herds (Chapters 1, 3 and 4) are similar to those reported in other arctic herds (Dauphiné 1976; Huot 1989; Allaye-Chan 1991). However, overwinter fat and protein losses of CAH females (Chapter 1) are substantially larger than those reported for herds with similar autumn fat reserves (Dauphiné 1976; Huot 1989; Allaye-Chan 1991). That large overwinter loss could have been caused by stochastic weather events, such as deep or early snow. If so, stochastic events may lead to expression of compensatory growth of females in the CAH. Therefore, I suggest a third

hypothesis regarding compensatory gains: moderately productive winter range in concert with a poor or moderately productive summer range prevents expression of compensatory growth. If energy availability in summer is inadequate (e.g., Chan-McLeod *et al.* 1994) a constant weight gain occurs, as in the PCH.

Ecological costs of lactation

In agreement with previous studies of mainland caribou (Dauphiné 1976; Huot 1989; Allaye-Chan 1991), females that raised a calf were unable to completely compensate for the costs of lactation and gestation by the rut in October. In my studies, nonlactating CAH females in autumn were 42% fatter and had 9% more protein than lactating females (Chapter 1), and nonlactating PCH females were 8% heavier and 82% fatter than their lactating counterparts in October (Chapter 4). However, lactating females apparently continued to deposit protein in autumn, since lactating PCH females were leaner, but not lighter, than nonlactating females in November. This finding is in contrast to the data of Allaye-Chan (1991), and suggests a propensity to enhance autumn protein and fat gains, although actual gains vary between years.

Nutrient availability in late autumn and early winter is likely important to the survival and reproductive potential of caribou. Eastland (1991) demonstrated that the autumn migration of PCH caribou is not directional; instead, caribou move in a "donut" ring surrounding Old Crow flats, utilizing the altitudinal gradients of the surrounding foothills to maximize intake and quality of forage during plant senescence. Stable isotope signatures ($\delta\ N^{15}/N^{14}$, $\delta\ C^{13}/C^{12}$) in caribou tissues support evidence that caribou eat mushrooms in autumn when they are available and that nitrogen from the mushrooms is incorporated into body protein (Barnette 1994). In addition, based on Cs^{137} accumulated in body tissues, White *et al.* (1993) suggested that autumn mushrooms provide a highly digestible, high-protein food source, allowing lactating females to gain additional fat and

protein prior to the rut. My data suggest that mushrooms and other nutritious autumn forages also might allow calves to grow longer, improving both the likelihood of overwinter survival and the probable future reproductive success of the cohort (Albon *et al.* 1987; Mech *et al.* 1991; Langvatn 1994).

Weaning

Weaning strategies of ungulates are flexible (Clutton-Brock *et al.* 1983; Lee *et al.* 1991). My data demonstrate that female caribou generally continue to lactate through the autumn rut (Chapter 3), unless weight gains are low enough to endanger survival: females that weaned early had lower than average over-summer gains (Table 11). I suggest that nearly all mature females ovulate and that the physiological decision of whether or not to implant is made immediately after the rut in most cases. Physiological decisions regarding pregnancy are related to timing of weaning.

Pregnancy

My research supports the generality that caribou are fecund: I found that only very lean females fail to ovulate (Chapter 3), in agreement with previous studies (Dauphiné 1976; Crête and Huot 1993) suggesting that mature female caribou ovulate unless in extremely poor condition. However, the controlling mechanism by which some embryos develop, and others are resorbed or rejected, is not understood. Dauphiné (1976) found numerous females that had ovulated in autumn and were not pregnant in early winter and suggested that early abortion was relatively common in caribou. In agreement, Gates *et al.* (1986) and Skogland (1984) reported evidence of *in utero* mortality. Progesterone assays from some PCH females in November indicated no pregnancy, while pregnancy-specific B concentrations attested that the females had been pregnant, suggesting early abortion (Russell *et al.* 1995). Therefore, data for the PCH

females sampled in November suggest that the 'decision' of whether to carry a zygote to term is made within 3-4 weeks after the rut.

In November, 2-4 weeks after the rut, probability of pregnancy for PCH caribou was directly correlated with both body weight and fat content. This result is in agreement with those from other species (e.g., Edey 1968; Albon *et al.* 1983a): fatter and heavier females are more likely to be pregnant. In addition, most pregnant female caribou were weaning their calves when captured in November. Females that had weaned early increased their probability of pregnancy from approximately 30% to 70% (Fig. 10) (assuming 4 kg of fat in autumn; Table 11). In contrast, females that had not weaned their calves (those that were extending lactation) were much less likely to be pregnant. This reduced fertility was not explained by differences in maternal body condition or skeletal size. Thus, the 'decision' to become pregnant involves lactation status: extending lactation reduces the probability of implanting an embryo and maintaining a pregnancy.

Lactational infertility

Decision processes in reproduction are probably derived from evolutionary strategies: the decision of whether or not to wean the current calf, increasing the probability of pregnancy, or to extend lactation, decreasing the likelihood of conception, is believed to balance evolutionary tradeoffs between maternal survival, calf reproductive potential, and lifetime reproductive output. However, the physiological mechanisms underlying such 'decisions' remain unclear. Both mother and offspring may interact to determine the timing of weaning and likelihood of pregnancy. For instance, I suggest that females extending lactation are exhibiting lactational infertility (Chapter 3). Perhaps suckling frequency of the calf causes an elevation of plasma prolactin levels, as seen in red deer (Loudon *et al.* 1983a), that interact with maternal body condition to reduce the likelihood of pregnancy. Thus, feedback from the calf could influence probability of

pregnancy. If this is the case, then females that fail to conceive may be more likely to continue lactating throughout winter, increasing the likelihood of the survival and subsequent reproductive success of their current calf. In support of this hypothesis, one nonpregnant CAH female killed in May was lactating and had a calf at heel (Table 2); similar incidences are reported in the literature (e.g., Shea 1979). In addition, late weaning may also be regulated, as a female might wean her calf during winter if her own survival was at risk.

Weaning strategies are the basis of parental investment theory for polygenous species. Females are expected to invest more in male than in female offspring (Trivers and Willard 1973). Lactation into or throughout winter is a form of maternal investment, which might be more common among mothers with male than female calves (Trivers 1974). In contrast, weaning of male calves during summer, when conditions do not allow both maternal body weight regain and lactation, may be an effective strategy, as these nutritionally disadvantaged males may never reach a "competitive" body size. On the other hand, females may still grow to reproductive body size, albeit more slowly. Thus, under some conditions it could be more advantageous to invest in female than male offspring.

Implications for population limitation and management

I have clarified some of the mechanisms by which female caribou might respond to differences in nutrient availability and body condition. I have shown that nutrition or resource availability can decrease probability of pregnancy both directly, through reductions of maternal body weight and fatness, and indirectly, through lactational infertility, most likely caused by changes in calf suckling behavior. Adequate body fat and protein content may therefore provide a nutritional cushion which decreases the sensitivity of a female to stochastic weather events and other sources of ecological stress, such as

harassment by insects or disturbance from petroleum development. As fatness is reduced, whether from density-dependent competition for resources or density-independent factors, productivity is expected to become increasingly sensitive to any environmental perturbations. A late greenup in spring is expected to reduce the milk production of a lean, light caribou, more than that of a heavier, fatter female. Because of lower milk production, the calf of the leaner female is expected to be unable to compensate for a low birth weight, may grow more slowly, and will enter winter with a lower body weight, thereby decreasing its probability of survival. Evidence from red deer studies suggests that low first-summer growth also may delay first reproduction. Similarly, deep winter snow is expected to reduce fetal growth and early milk production more dramatically in females which had marginally adequate body reserves to become pregnant.

For the PCH, Russell *et al.* (1995) showed that stochastic weather events have a powerful effect on likelihood of pregnancy. I demonstrated that the effect of weather on pregnancy rate is mediated by changes in body condition and lactation status. However, I have no definitive evidence for, or against, a density-dependent effect in this huge (175,000; Fancy *et al.* 1994) herd. In contrast, environmental perturbations in the CAH may have larger impacts, as there is putative evidence of density-dependent reductions in pregnancy rate for this herd (Cameron 1995).

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APPENDIX I

Appendix 1. Data used for analyses in Chapter 1. Animal identification number (ID), age (adult, fetus, or age in days; AGE), sex (0 = male, 1 = female), body weight (kg, less antlers and concepta; BW), ingesta-free body weight (kg, IFBW), carcass weight (kg, CW), water content of the ingesta-free body (kg, WTR), fat content (kg, FAT), ash content (kg, ASH), protein content (kg, PTN), metatarsus length (cm, MET), mandible length (cm, MAND), heart weight (g, HW), liver weight (g, LW), empty gastro-intestinal tract weight (g, GI), and weight of kidneys (g, KW). For breakdown of subspecies and seasons in which adults were collected, see Appendix II.

ID	AGE	SEX	BW	IFBW	CW	WTR	FAT	ASH	PTN	MET	MAND	HW	LW	GI	KW
13	adult	0	138.7	118.6	77.4	62.98	20.78	9.02	25.78	35	30.2	105	254	979	38
BK	adult	0	132.2	115.8	76	64.4	14.8	10.28	26.33	35		120	225	975	33
855	adult	0	70	55.6	35.9	36.24	2.08	4.76	12.54	28		66	85	399	15
837	adult	0	99.7	85.9	51.6	55.2	3.29	8.27	19.11	30		97	146	493	25
M	adult	0	113.9	99.6	64	59.34	8.25	9.7	22.35	30		122	195	671	34
28	adult	0	87.2	76.5	47.6	48.62	3.38	6.01	18.45	36.5		83	159	542	29
856	adult	0	82	67.2	39.2	43.05	2.13	6.93	15.05	35		85	134	563	24
R	adult	0	121.3	104.1	63.8	58.05	16.86	8.45	20.71	34		127	181	993	32
25	adult	0	118.5	99.3	62.9	54.2	18.02	9.15	17.91	36		117	171	876	33
50	adult	0	205.6	191	121.3	101.02	41.15	16.96	31.9	41.4	32.7	150	350	1407	62
80	adult	1	84.1	70.7	40.7	45.54	3.05	3.71	18.41		27.7	146	171	632	27
81	adult	1	95.8	79.6	50	48.62	5.08	6.75	19.11	38.1	27.6	171	183	721	27
82	adult	1	92.6	71.5	45.8	45.4	4.15	4.93	17.05	39.4	26.6	117	159	633	24
83	adult	1	80.2	68.4	42.5	38.87	7.84	3.6	18.1	38.1	27.5	108	134	660	18

Appendix I. cont.

ID	AGE	SEX	BW	IFBW	CW	WTR	FAT	ASH	PTN	MET	MAND	HW	LW	GI	KW
84	adult	1	96.6	83.3	48.1	48.16	9.18	6.19	19.79	38.5	27.2	125	181	865	22
100	adult	1	57.1	51.4	31.6	32.81	3.62	3.45	11.5	39	25.6	70	81	325	12
102	adult	1	72.8	65.2	38.5	41.77	4.82	4.93	13.66	38.6		88	71	379	14
103	adult	1	67.3	61.5	36.7	39.36	2.38	5.14	14.67	39		78	93	434	17
104	adult	1	65.6	60.4	34.3	38.79	3.36	4.36	13.93	39.4		70	77	395	16
107	adult	1	69.4	56.3	36.5	36.6	2.37	4.13	13.21	38.4		88	97	465	17
108	adult	1	78.6	69.6	43.3	43.78	5.41	4.93	15.46	38		100	79	367	13
112	adult	1	76.8	63.6	41.6	42.58	2.27	4.03	14.74	39		112	195	608	34
114	adult	1	76.8	61.8	41.3	41.96	1.42	4.29	14.13	39.2	28.2	73	180	673	33
115	adult	1	80	65.3	38.6	43.43	1.28	4.57	16.04	38.2	26.6	100	217	843	34
117	adult	1	70	52.7	32	34.46	1.57	3.95	12.74	37.3	26.4	88	201	592	30
90	fetus	0	2.8	2.8	1.6	2.13	0.05	0.13	0.46	17.8	10.5	4	8	9	2
91	fetus	1	3.3	3.3	1.8	2.49	0.08	0.11	0.57	19.8	10.6	4	8	11	3
92	fetus	0	2.8	2.8	1.6	2.13	0.04	0.13	0.47	19.1	10.8	5	7	9	2
93	fetus	0	3.3	3.3	1.8	2.56	0.06	0.14	0.56	19.8	11.4	4	7	10	2
94	fetus	1	3.2	3.2	1.8	2.47	0.08	0.14	0.5	17.8	10.2	3	7	7	3
120	0	0	6.4	6.2	4	4.68	0.13	0.27	1.13	25.8	13.3	8	16	31	4
121	0	0	6.2	5.9	3.8	4.45	0.13	0.24	1.05	25.4	12.6	9	16	33	3
122	0	1	4.9	4.7	2.7	3.58	0.12	0.21	0.83	23.9	12.5	6	15	30	3
124	0	0	6.4	6.2	4	4.69	0.16	0.28	1.1	25.1	12.6	8	16	32	3
125	0	1	5.4	5.2	3.1	3.88	0.19	0.21	0.9	23.2	11.7	9	19	37	4

Appendix I. cont.

ID	AGE	SEX	BW	IFBW	CW	WTR	FAT	ASH	PTN	MET	MAND	HW	LW	GI	KW
126	0	0	5.3	5.2	3.3	3.87	0.11	0.26	0.92	24.5	13.3	8	13	25	3
127	0	0	5.7	5.5	3.3	4.17	0.13	0.22	1.02	24.5	12.2	7	17	32	3
128	0	0	5.4	5.3	3.5	3.94	0.13	0.26	0.99	25.3	12.7	8	12	21	3
129	0	0	4.5	4.3	2.5	3.22	0.07	0.19	0.77	22.9	12	6	10	19	3
130	0	0	6.3	6.2	4.1	4.57	0.12	0.36	1.15	25.4	12.7	9	13	21	3
131	0	1	5.4	5.4	3.4	3.72	0.47	0.29	0.87	26	13.3	8	13	30	4
132	0	0	4.8	4.7	2.9	3.64	0.05	0.2	0.84	24.7	12.6	8	12	18	3
133	0	0	6.1	6	4	4.59	0.05	0.28	1.11	27.2	12.4	11	20	27	4
134	0	0	4.9	4.9	2.9	3.66	0.08	0.25	0.87	24.4	13.3	8	12	27	4
135	0	1	3.1	3.1	1.8	2.41	0.04	0.12	0.56	22	10.2	5	8	16	3
136	21	1	14.5	13.8	9.7	9.95	0.44	0.66	2.73	29.4	15.1	30	33	56	7
137	21	0	17.1	16.1	11.7	11.41	0.87	0.81	3.05	29.5	16	37	47	73	9
138	21	0	17.6	16.6	11.5	12	0.57	0.77	3.22	29	15.4	33	45	68	9
139	21	0	13.5	13	9	9.43	0.42	0.64	2.56	28.4	14.8	25	32	50	7
140	21	0	12.6	12	8.3	8.57	0.5	0.56	2.34	26.8	14.3	19	32	52	6
141	21	1	17.7	16.3	10.8	11.46	0.89	0.85	3.1	28.3	15.3	23	37	65	10
142	24	1	17.1	16	11.7	11.53	0.54	0.8	3.13	31.2	15.4	27	42	58	9
145	24	1	16	14.6	10.3	10.29	0.69	0.75	2.87	29	14.7	22	43	53	7
146	44	0	16.1	13.7	9.2	10.12	0.12	0.69	2.79	26.3	14.9	22	30	78	7
147	44	1	22.1	19.3	14.1	13.91	0.56	0.96	3.91	28.9	16.2	32	43	87	13
143	24	0	20.6	19.1	13.5	13.6	0.8	0.93	3.74	29.9	15.9	30	61	75	14

Appendix I. cont.

ID	AGE	SEX	BW	IFBW	CW	WTR	FAT	ASH	PTN	MET	MAND	HW	LW	GI	KW
144	24	1	17.5	16.6	11.9	11.33	1.36	0.87	3.07	28.3	15.6	30	48	75	10
148	44	0	25.5	22.5	15.7	16.23	0.48	1.07	4.74	30.3	17.6	35	48	96	12
149	44	0	22.2	19.6	13.1	14.48	0.27	0.94	3.91	28.4	16.1	27	48	86	11
150	44	1	23	20.8	14.2	15.23	0.37	1.07	4.18	30.3	16.6	35	45	109	10
151	44	0	15.9	14.4	9.5	10.66	0.16	0.68	2.85	28.8	15.1	21	30	72	7
152	44	0	25.9	23.4	15.4	16.76	0.64	1.34	4.71	30.2	17	36	59	111	11
153	44	0	20.7	18.5	12.5	13.32	0.41	0.95	3.78	29.5	15.9	28	45	85	9
154	44	1	26	23.1	15.7	16.66	0.51	1.23	4.73	30.6	16.6	36	65	129	12
155	44	0	23.6	20.2	13.6	14.67	0.25	1.04	4.25	30.7	17.3	30	59	121	12
160	102	1	36.8	32.4	21	21.89	1.18	1.79	7.54	32.7	19.6	46	70	279	9
161	102	1	46.7	38.5	24.9	26.12	1.76	2.02	8.56	33.9	20.6	52	73	273	13
162	102	1	46	39.3	26.6	25.95	2.43	2.33	8.59	34.3	20.7	45	74	254	12
163	102	0	48.2	40.5	28	26.41	2.76	2.54	8.75	34.3	21.3	46	71	255	14
164	102	1	41.2	37.2	22.7	25.19	1.61	1.94	8.5	33.2	19.8	52	76	386	13
166	134	1	43.1	38	26.1	24.78	2.6	2.14	8.46	32.3	20.3	48	66	326	10
167	134	1	37	29	18.7	19.85	1.13	1.46	6.54	32.3	19.6	33	55	209	8
168	134	1	30.8	23.8	15.3	16.88	0.56	1.19	5.13	32.2	18.2	34	44	203	8
169	134	0	52.5	44.5	27.6	28.98	3.09	2.58	9.83	34.9	21.8	59	76	289	13
170	134	0	55.1	46.9	32.2	29.86	4.5	2.98	9.58	35.4	21.4	65	77	299	13
171	134	0	46.8	38.1	27	25.28	2.22	2.33	8.32	34	21.7	54	59	244	11
172	134	1	48.1	40.3	27.9	26.65	2.69	2.16	8.78	33.8	20.6	59	86	271	11

Appendix I, cont.

ID	AGE	SEX	BW	IFBW	CW	WTR	FAT	ASH	PTN	MET	MAND	HW	LW	GI	KW
173	134	0	47.8	39.5	26	26.52	1.95	2.06	8.98	34.3	21.2	46	76	261	14
174	134	1	38.8	31.6	20.3	20.77	2.01	1.7	7.12	32.3	20.1	35	64	237	11
175	134	0	49.6	43.3	28.6	28.29	3.16	2.64	9.23	35.7	21.7	56	76	290	12

APPENDIX II

Appendix II: Data used for analyses in Table 6 and Figure 7, Chapter 2. Animal identification (ID), classification group (GROUP), body condition score (BCS), body weight (BW, kg), body reserves index (BRI = BCS * BW), and fat content (kg, from Chapter 1). Classification groups are defined as: Group 0, caribou calves; Group 1, adult female caribou in October; Group 2, adult female caribou in May; Group 3, adult female caribou in July; and Group 4, adult male reindeer.

ID	GROUP	BCS	BW	BRI	FAT
13	4	10	138.7	1387	20.8
BK	4	8	132.2	1058	14.8
855	4	5	70.0	315	2.1
837	4	4	99.7	399	3.3
M	4	8	114.8	861	8.2
28	4	6	88.3	530	3.4
856	4	7	83.2	541	2.1
R	4	10	121.3	1213	16.9
25	4	9	118.5	1067	18.0
50	4	15	209.8	3147	41.1
80	1	9	84.3	758	3.0
81	1	9	96.0	864	5.1
82	1	8	92.7	695	4.1
83	1	12	80.3	963	7.8
84	1	12	97.1	1165	9.2
100	2	6	64.0	384	3.6
102	2	8	78.2	586	4.8
103	2	7	73.2	476	2.4
104	2	6	72.2	397	3.4

Appendix II, cont.

ID	GROUP	BCS	BW	BRI	FAT
107	2	5	69.5	347	2.4
108	2	8	84.6	677	5.4
112	3	4	76.8	269	2.3
114	3	5	76.8	384	1.4
115	3	5	80.0	360	1.3
117	3	5	70.0	350	1.6
120	0	9	6.4	58	0.1
121	0	8	6.2	46	0.1
122	0	8	4.9	37	0.1
124	0	11	6.4	67	0.2
125	0	9	5.4	49	0.2
126	0	9	5.3	48	0.1
127	0	9	5.7	51	0.1
128	0	9	5.4	49	0.1
129	0	8	4.5	34	0.1
130	0	8	6.3	47	0.1
132	0	5	4.8	22	0.0
133	0	5	6.1	27	0.1
134	0	5	4.9	22	0.1
135	0	3	3.1	9	0.0
136	0	8	14.5	109	0.4
137	0	8	17.1	128	0.9
138	0	8	17.6	141	0.6
139	0	8	13.5	101	0.4
140	0	8	12.6	101	0.5

Appendix II, cont.

ID	GROUP	BCS	BW	BRI	FAT
141	0	8	17.7	141	0.9
142	0	8	17.1	128	0.5
143	0	9	20.6	185	0.8
144	0	9	17.5	149	1.4
145	0	8	16.0	120	0.7
146	0	8	16.1	129	0.1
147	0	10	22.1	210	0.6
148	0	9	25.5	217	0.5
149	0	9	22.2	189	0.3
150	0	9	23.0	196	0.4
151	0	8	15.9	127	0.2
152	0	10	25.9	246	0.6
153	0	9	20.7	176	0.4
154	0	9	26.0	234	0.5
155	0	8	23.6	189	0.3
160	0	7	36.8	258	1.2
161	0	7	46.7	327	1.8
162	0	8	46.0	345	2.4
163	0	8	48.2	361	2.8
164	0	8	41.2	309	1.6
166	0	8	43.1	345	2.6
167	0	8	37.0	277	1.1
168	0	7	30.8	200	0.6
169	0	8	52.5	420	3.1
170	0	8	55.1	441	4.5

Appendix II, cont.

ID	GROUP	BCS	BW	BRI	FAT
171	0	7	46.8	328	2.2
172	0	8	48.1	385	2.7
173	0	8	47.8	359	2.0
174	0	8	38.8	310	2.0
175	0	8	49.6	397	3.2

APPENDIX III

Appendix III. Data used for analyses in Figure 8, Chaper 2, and all of Chapter 3. Identification numbers of adult Porcupine herd females (ID), year of capture (0 = 1990; 1 = 1991; and 2 = 1992; YR), body weight (BW, kg), body condition score (BCS), body reserves index (BRI = BCS * BW), milk in the mammary (presence (1) or absence (0); MILK), pregancy status (0 = notpregnant; 1 = pregnant; PREG), pregnancy category (0 = $Progesterone^{-}/PSPb^{-}$; 1 = $Progesterone^{+}/PSPb^{+}$; 2= $Progesterone^{+}/ PSPb^{-}$; 3 = $Progesterone^{-}/PSPB^{-}$; PREGCAT), lactation class (0 = extending lactation; 1 = ceasing lactation; 2 = nonlactating; LACT), fat content (kg, from equation 1, Chapter 3; FAT), protein content (kg, from equation 2, Chapter 3; PTN), mandible length (cm; MAND), metatarsus length (cm; MET), and age class (AGE, 0 = yearling (excluded from analyses), 1 = young; 2 = medium; 3 = old).

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
1	0	93.0	7.0	651.0	1	0	3	1	5.18	17.79	29.8	39.7	
2	0	103.0	9.5	978.5	0	1	1	2	9.33	19.77	28.9	40.9	2
3	0	109.0	9.0	981.0	0	1	1	2	9.36	20.96	28.2	41.2	
4	0	76.0	6.5	494.0	1	0	0	0	3.48	14.44	28.4	39.6	1
5	0	84.0	6.5	546.0	1	1	1	1	4.02	16.01	27.6	39.4	
6	0	101.0	7.0	707.0	1	1	2	1	5.83	19.37	27.1	39.7	
7	0	93.0	7.0	651.0	0	1	2	2	5.18	17.79	27.3	38.9	2
8	0	94.0	9.5	893.0	0	1	1	2	8.18	17.98	27.7	38.9	2
9	0	82.0	7.5	615.0	1	0	3	0	4.77	15.62	27.1	39.3	
10	0	81.0	7.0	567.0	1	1	1	1	4.24	15.42	27.9	39.7	2

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
11	0	94.0	8.5	799.0	0	1	1	2	6.96	17.98	28.4	38.9	
12	0	77.0	6.5	500.5	1	1	1	1	3.54	14.63	27.2	39.0	2
13	0	96.0	6.5	624.0	1	1	1	1	4.87	18.38	26.8	40.9	3
14	0	79.0	6.5	513.5	1	1	1	1	3.68	15.03	26.7	38.6	1
15	0	79.0	7.5	592.5	1	1	1	1	4.52	15.03	27.6	38.0	1
16	0	77.0	7.5	577.5	0	1	1	2	4.36	14.63	27.0	40.2	1
17	0	87.0	5.0	435.0	1	1	1	1	2.89	16.60	28.0	39.9	
18	0	95.0	7.0	665.0	1	1	1	1	5.34	18.18	29.0	39.8	2
19	0	88.0	7.5	660.0	0	1	1	2	5.28	16.80	27.2	40.5	1
20	0	100.0	6.5	650.0	0	1	1	2	5.17	19.17	29.0	40.7	2
21	0	88.0	7.5	660.0	0	1	1	2	5.28	16.80	26.6	39.8	1
22	0	88.0	5.5	484.0	1	0	3	1	3.38	16.80	27.4	40.1	2
23	0	94.0	5.5	517.0	1	0	3	0	3.71	17.98	29.2	41.1	2
24	0	78.0	7.0	546.0	0	1	1	2	4.02	14.83	25.5	37.6	1
25	0	81.0	6.0	486.0	1	1	1	1	3.40	15.42	26.6	39.7	1
26	0	82.0	6.0	492.0	0	1	2	2	3.46	15.62	25.8	39.7	2
27	0	91.0	8.0	728.0	0	1	1	2	6.09	17.39	27.0	39.6	1
28	0	77.0	6.5	500.5	1	1	1	1	3.54	14.63	26.0	40.1	1

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
29	0	80.0	7.0	560.0	1	0	3	1	4.17	15.22	25.4	40.1	1
30	0	94.0	6.5	611.0	1	1	1	1	4.73	17.98	28.2	40.6	3
31	0	83.0	9.5	788.5	0	1	1	2	6.83	15.81	26.1	37.9	1
32	0	87.0	7.5	652.5	0	1	1	2	5.20	16.60	27.6	40.4	1
33	0	84.0	7.5	630.0	0	1	1	2	4.94	16.01	25.2	37.5	1
34	0	90.0	7.5	675.0	1	1	1	1	5.46	17.19	26.1	38.3	1
35	0	80.0	6.0	480.0	1	1	1	1	3.33	15.22	27.6	37.6	
36	0	88.0	6.5	572.0	1	0	0	0	4.30	16.80	27.3	39.9	2
37	0	82.0	7.0	574.0	1	1	1	1	4.32	15.62	28.4	37.7	1
38	0	96.0	5.5	528.0	1	1	1	1	3.83	18.38	27.2	38.4	2
39	0	77.0	7.0	539.0	1	1	1	1	3.94	14.63	23.0		1
40	0	77.0	5.0	385.0	1	0	0	1	2.43	14.63	26.3	38.0	1
41	0	95.0	7.0	665.0	1	1	1	1	5.34	18.18	27.0	39.8	2
42	0	87.0	6.0	522.0	1	0	3	1	3.76	16.60	27.6	40.8	2
43	0	91.0	5.0	455.0	1	1	1	1	3.09	17.39	28.6	40.0	1
44	0	102.0	7.0	714.0	1	1	1	1	5.92	19.57	28.5	41.0	
45	0	81.0	7.5	607.5	1	0	3	1	4.69	15.42	26.7	39.7	1
46	0	97.0	8.0	776.0	1	1	1	1	6.67	18.58	28.0	40.6	2

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
47	0	95.0	7.0	665.0	1	1	1	0	5.34	18.18	28.2	40.6	3
48	0	93.0	7.5	697.5	1	1	1	1	5.72	17.79	28.8	38.3	2
49	0	77.0	5.0	385.0	1	0	0	0	2.43	14.63	27.7	40.0	1
50	0	93.0	5.5	511.5	1	1	1	1	3.66	17.79	27.2	39.8	2
51	0	81.0	5.5	445.5	1	1	1	0	2.99	15.42	26.7	40.3	2
52	0	80.0	6.5	520.0	1	1	1	1	3.74	15.22	25.2	40.2	
53	0	91.0	6.5	591.5	1	1	1	1	4.51	17.39	27.6	40.6	2
54	0	98.0	8.0	784.0	0	1	1	2	6.77	18.78	28.3	38.8	2
55	0	83.0	7.0	581.0	1	0	3	0	4.39	15.81	27.1	39.4	1
56	0	87.0	5.0	435.0	1	1	1	1	2.89	16.60	27.2	39.7	2
57	0	86.0	8.0	688.0	1	1	1	1	5.61	16.40	28.0	37.9	
58	0	99.0	6.5	643.5	1	1	1	1	5.09	18.97	28.3	40.5	2
59	0	82.0	4.5	369.0	1	0	3	0	2.28	15.62	27.5	39.9	2
60	0	99.0	6.0	594.0	1	1	1	1	4.54	18.97	28.0	40.1	2
61	1	110.0	7.0	770.0	1	1	2	1	6.60	21.16	28.0	38.2	
62	1	106.0	9.0	954.0	1	1	1	1	8.99	20.36	27.8	40.0	
63	1	89.0	8.5	756.5	1	1	1	1	6.43	17.00	26.7	37.1	
64	1	94.0	7.0	658.0	1	0	0	0	5.26	17.98	27.3	39.6	

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
65	1	99.0	5.0	495.0	1	0	0	0	3.49	18.97	28.9	39.1	
66	1		9.0	1	1	2	1						
67	1	104.0	9.0	936.0	1	0	0	0	8.75	19.96	26.8	40.2	
68	1	104.0	5.0	520.0	1	0	0	0	3.74	19.96	26.2	39.2	
69	1	93.0	8.0	744.0	1	1	1	1	6.28	17.79	26.2	39.5	
70	1	102.0	9.5	969.0	1	1	2	1	9.20	19.57	25.4	39.0	
71	1	102.0	9.0	918.0	0	1	1	2	8.51	19.57	27.3	39.1	
72	1		9.5	0	1	1	2						
73	1	84.0	8.5	714.0	1	0	0	0	5.92	16.01	24.8	38.6	
74	1		9.5		0	1	1	2					
75	1	94.0	10.0	940.0	1	1	1	1	8.80	17.98	27.8	38.4	
76	1	102.0	11.0	1122.0	0	1	1	2	11.37	19.57	27.8	39.8	
77	1	97.0	9.5	921.5	1	1	1	1	8.55	18.58	27.0	39.0	
78	1	110.0	9.5	1045.0	0	1	2	2	10.26	21.16	27.3	39.6	
79	1		5.5		1	1	2	0					
80	1	104.0	7.5	780.0	0	1	1	2	6.72	19.96	28.8	40.5	
81	1	95.0	5.5	522.5	1	1	1	0	3.77	18.18	29.9	40.0	
82	2	100.7	6.0	604.1	1	0	0	0	4.65	19.31	28.1	40.3	3

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
83	2	87.5	8.5	744.0	0	1	2	2	6.28	16.71	27.2	38.4	1
84	2	97.5	6.0	585.0	1	1	2	0	4.44	18.68	28.1	38.9	2
85	2	98.0	8.5	832.7	0	1	2	2	7.39	18.77	28.0	40.5	1
86	2	89.3	7.5	670.1	1	1	2	0	5.40	17.06	26.2	39.2	1
87	2	95.7	7.5	717.7	1	1	2	0	5.96	18.32	26.7	40.7	2
88	2	88.0	8.5	747.8	0	1	2	2	6.33	16.80	26.9	38.8	1
89	2	78.9	6.0	473.5	1	1	2	0	3.27	15.01	27.4	40.0	1
90	2	95.2	8.5	809.5	1	1	2	0	7.09	18.23	27.1	39.8	2
91	2	84.8	8.0	678.5	1	1	2	1	5.50	16.17	26.3	37.7	3
92	2	93.4	8.0	747.4	1	1	2	1	6.32	17.87	27.6	40.1	2
93	2	97.1	8.0	776.4	1	1	1	1	6.68	18.59	28.3	40.0	2
94	2	93.4	7.5	700.7	1	1	2	0	5.76	17.87	26.5	40.2	1
95	2	82.1	7.5	615.6	1	1	2	1	4.78	15.63	26.6	38.9	1
96	2	88.4	8.0	707.5	1	1	2	1	5.84	16.89	27.0	39.4	2
97	2	74.4	8.5	632.2	0	0	0	2	4.96	14.12	25.6	39.7	1
98	2	80.7	7.5	605.4	0	0	0	2	4.66	15.37	26.6	40.1	1
99	2	86.2	7.5	646.3	1	0	0	0	5.12	16.44	26.6	39.6	1
100	2	66.7	8.5	566.7	0	0	0	2	4.24	12.61	24.3	37.9	0

Appendix III, cont.

ID	YR	BW	BCS	BRI	MILK	PREG	PCAT	LACT	FAT	PTN	MAND	MET	AGE
101	2	75.3	7.5	564.6	0	0	0	2	4.22	14.30	25.1	39.5	1
102	2	95.2	7.0	666.7	1	1	2	0	5.36	18.23	28.8	40.5	3
103	2	95.7	6.0	574.1	1	1	2	1	4.32	18.32	28.2	40.3	1
104	2	98.9	7.0	692.1	1	1	2	0	5.66	18.95	27.6	39.2	2
105	2	84.4	7.0	590.5	1	1	2	0	4.50	16.08	27.6	40.5	2
106	2	83.9	6.5	545.4	1	0	0	0	4.01	15.99	26.7	39.0	1
107	2	88.9	7.0	622.2	1	1	2	0	4.85	16.97	27.7	39.0	2

APPENDIX IV

Appendix IV. Data used for analyses in Chapter 4. Identification numbers of wild and captive adult female caribou of the Porcupine herd (ID), lactation status (0 = nonlactating, 1 = lactating; LAC), body weight in June/July (kg, JBW), body condition score in June/July (JBCS), estimated body fat (kg, from equation 1, Chapter 2; JFAT), body weight in October (kg, OBW), body condition score in October (OBCS), estimated body fat (kg, from equation 1, Chapter 2; OFAT), weight gain from June to October (kg; GAIN), rate of weight gain from June to October (g/d; GD), and fat gain from June to October (kg, FGN).

ID	LAC	JBW	JBCS	JFAT	OBW	OBCS	OFAT	GAIN	GD	FGN
92108	1	80.3	3.5	1.5	92.5	4.5	2.6	12.2	122.5	1.1
92106	1	90.7	4.0	2.2	100.2	6.0	4.5	9.5	95.2	2.3
92105	1	79.8	4.5	2.1	87.5	7.5	5.1	7.7	77.1	3.0
92104	1	77.1	4.5	2.0	84.8	7.5	4.9	7.7	77.1	2.8
92103	1	80.7	4.5	2.2	92.5	6.5	4.5	11.8	117.9	2.3
92102	1	78.0	4.0	1.8	96.2	6.5	4.8	18.1	181.4	3.0
9298	1	69.4	4.5	1.8	85.3	7.0	4.4	15.9	158.7	2.7
9297	1	71.2	4.0	1.5	84.4	4.5	2.3	13.2	131.5	0.8
9296	1	89.8	4.0	2.1	102.0	5.0	3.5	12.2	122.5	1.4
9294	1	78.2	5.0	2.4	85.3	4.5	2.4	7.0	70.3	-0.1
9293	1	63.5	5.0	1.8	74.4	7.0	3.7	10.9	108.8	1.9
9287	1	83.4	6.5	3.9	91.6	7.5	5.4	8.2	81.6	1.6
9106	0	81.2	6.0	3.3	98.9	10.0	9.2	17.7	176.9	5.9
9012	0	73.5	4.5	1.9	86.6	10.0	7.6	13.2	131.5	5.7
9004	0	75.3	6.0	3.0	91.6	7.5	5.4	16.3	163.3	2.5
92214	0	80.3	6.0	3.3	93.9	8.0	6.2	13.6	136.1	2.9
92212	0	82.5	4.5	2.2	99.8	6.5	5.0	17.2	172.3	2.8

Appendix IV, cont.

ID	LAC	JBW	JBCS	JFAT	OBW	OBCS	OFAT	GAIN	GD	FGN
92210	0	81.6	7.0	4.2	97.1	8.0	6.5	15.4	154.2	2.3
92209	0	92.1	6.5	4.5	107.5	10.5	11.1	15.4	154.2	6.7
92208	0	88.4	5.5	3.3	103.4	7.0	5.9	15.0	149.7	2.6
92207	0	75.7	5.5	2.7	95.7	8.0	6.4	20.0	199.6	3.7
92206	0	92.5	4.5	2.6	104.8			12.2	122.5	
92205	0	88.0	4.0	2.1	101.1	8.0	6.9	13.2	131.5	4.8
92204	0	81.2	6.0	3.3	93.4	9.0	7.3	12.2	122.5	4.0
92201	0	73.0	5.5	2.5	87.1	8.5	6.1	14.1	140.6	3.5
92202	0	77.6	5.5	2.8						
92203	0	73.5	6.0	2.9						
92211	0	85.3								
92213	0	83.4	5.0	2.7						
9007	0	78.9	3.5	1.5						
9013	0	99.3	6.5	5.1						
9016	0	88.4	7.5	5.3						
9281	1	72.6	6.0	2.9						
9282	1	79.4	4.5	2.2						
9283	1	77.1	4.0	1.8						
9284	1	68.5	4.5	1.8						
9285	1	74.8	3.0	1.1						
9288	1	84.4	5.5	3.2						
9289	1	80.3	5.5	2.9						
9290	1	82.1	4.5	2.3						
9291	1	83.9	5.0	2.7						
9292	1	80.3	5.5	2.9						

Appendix IV, cont.

ID	LAC	JBW	JBCS	JFAT	OBW	OBCS	OFAT	GAIN	GD	FGN
9295	1	73.5	4.5	1.9						
9299	1	72.6	4.5	1.9						
92100	1	81.6	4.5	2.3						
92107	1	72.6	5.0	2.2						
92109	1	93.4	3.5	1.9						
92101	1	78.9	3.5	1.5						
9286	1	88.9	5.0	3.0						
Ptar	1	95.2			111.6			16.3	163.3	
Brooks	1	87.5			107.5			20.0	199.6	
Pingo	1	92.1			111.6			19.5	195.0	
Pokok	1	106.6			120.2			13.6	136.1	
Gentn	1	83.9			103.4			19.5	195.0	
Hula	1	102.5			117.9			15.4	154.2	
Hemlock	1	83.9			99.8			15.9	158.7	

APPENDIX V

Appendix V. Data used for analyses of calf growth in Chapter 4. Identification number of maternally raised Porcupine Herd caribou at the Large Animal Research Station, University of Alaska Fairbanks (ID numbers 1-20), and free-ranging maternally raised calves of the Porcupine Caribou Herd (ID numbers 9201-9280), calf sex (0 = male, 1 = female), birth weight (kg, 0BW), and body weight at approximately 3, 6, 15, and 19 weeks of age (kg, 3BW, 6BW, etc).

ID	SEX	0BW	3BW	6BW	15BW	19BW
1	0	7.73		26.3		72.11
2	0	6.82	17.23	19.95	47.62	54.88
3	0	6.36		22.22		45.35
4	0	5.90	18.59	24.04	44.44	
5	0	7.27	15.87	28.57	51.7	67.12
6	0	5.91	19.05	23.58		51.25
7	0	6.82				71.66
8	0	7.27	16.78	21.32	52.15	67.12
9	0	7.27				
10	0	9.09				
11	0	8.18	19.95	25.4	42.18	53.51
12	0	9.09	19.05	28.57	53.06	57.6
13	1	4.50	18.59	21.32	45.35	
14	1	7.73	14.97	21.77	48.07	56.69
15	1	6.36		16.32		50.79
16	1	6.82	15.87	19.05	42.18	48.07
17	1	5.50	11.80	17.7	38.2	
18	1	8.18	14.97			49.89
19	1	6.82	19.05			55.33

Appendix V, cont.

ID	SEX	0BW	3BW	6BW	15BW	19BW
20	1	5.91	11.34	17.23		40.36
21	1	7.27	18.14			48.53
22	1	6.36	18.14	21.32		56.69
9201	0	6.6	16.1			
9202	0	6.2	17.0	22.9	44.4	
9205	1	6.5	15.0	21.1		
9207	0	5.5	14.8	18.4	40.0	
9209	1	5.3	14.3		32.7	
9210	1	4.8	15.0		39.0	
9211	0	5.8	13.8			
9212	0	6.3	15.9	21.1		
9215	0	6.5	16.6			
9216	1	6.4	14.7	21.1		
9218	0	7.9	19.7			
9219	0	6.1	17.3		45.4	
9222	0	7.3	17.5			
9226	0	6.9	17.5			
9227	1	7.0	15.6	21.1	40.4	
9230	0	6.1	14.8		39.9	
9231	1	5.5	12.9	19.7		
9235	0	7.7	20.7		52.2	
9239	0	7.7	19.3			
9241	0	6.6	17.9			
9242	1	5.7	14.2		38.1	
9246	1	7.3	14.3			

Appendix V, cont.

ID	SEX	0BW	3BW	6BW	15BW	19BW
9248	0	6.9	13.4			
9252	1	6.4	15.9	21.5		
9254	1	6.9	15.6			
9257	0	6.6	12.9			
9258	0	6.8			50.3	
9259	0	6.9	16.8	23.8		
9260	0	7.8			43.1	
9261	0	8.3	15.2			
9265	1	6.2	13.4			
9265	1	6.2		20.2		
9266	0	7.1	15.2			
9267	0	6.5	14.6	21.5	45.8	
9268	0	5.4	15.6			
9270	0	5.3	13.8			
9271	0	5.6	13.4			
9272	1	5.8	12.5			
9273	1	5.5	12.9			
9275	0	5.9	14.1	17.5		
9280	0	6.1	14.7	15.7		